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Semantic processing of natural and artificial entities

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PhD Thesis

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ACKNOWLEDGEMENTS
The unquantifiables

I am certain that if memory would permit, an extensive and determinate number of life's offerings could be calculated for each of the people that have made these past 5 years, in some moments tolerable, in others of the most rewarding, and in others still, quite frankly, livable. However, there is no determinate quantity that can be placed neither on the meaning of these moments nor on the warmth that pervades my heart. There are those that would consider obtaining a PhD as one of the greatest achievements in life; yet it is without a doubt that it is the people whom I've encountered along the way that have provided the greatest testament to my existence. Each and every one of them has satisfied a Maslowian need at some point, from the most basic to the most profound. And it is from them that I've learned how to live more generously, more conscientiously, more patiently, more *thoroughly*.

There are the ones that have stood at the core, that have provided a pillar of stability when it was difficult to find one within myself. They have been a comfort and a joy, both from close and from afar.

"For that which you love most [in your friend] may be clearer in his absence, as the mountain to the climber is clearer from the plain." --*Gibran*

Existence can be effortful and yet indifferent. Though no matter life's offerings or demands, I have been lucky enough to be cared for and considered in the highest regard, and it is through this kindness that I found my fuel and my nourishment.

"For it is his to fill your need, but not your emptiness.
And in the sweetness of friendship let there be laughter, and sharing of pleasures.
For in the dew of little things the heart finds its morning and is refreshed." --*Gibran*

I would like to thank my mentors for offering strength and encouragement, patience and wisdom, which has led to my growth, not only in the academic sphere, but also as an individual in facing my limitations and challenges in life.

And then there is my father, for whom there is no thank you big enough. He is a modest man, a simple man, a man whose heart is bigger and wisdom vaster than anyone I know. While I have been cushioned in my ivory tower, it is he who has faced life with all of the virtues necessary for what it means to truly succeed. I hope that I can face the world with even half the ability to relate and to sacrifice as he has shown.

All of you remain as noumena of my heart, outside of time and space, as transcendental fibers of my being...

GENERAL INTRODUCTION

The representation of concepts in everyday life has been investigated for as long as the meaning of life itself. The permanence of objects in space and their transformation in light of the passage of time have long preoccupied the minds of philosophers. Aristotle first queried the nature of form and matter through an intuitive division of the world into natural kinds and artifice, focusing on the persistence of entities throughout transformations in their properties (Aristotle, trans. 1983). Spinoza offered a more systematic breakdown of a triad in the conceptual framework- ideas (concepts), images, and words- and cautioned against the erroneous transmittance of meaning when there is confusion between a concept *per se* and the images and words by which we denote it (Jongeneelen, 2001). The relationship between the generation of 'images' in the mind and the epistemological experience in the real world is one of central importance to the understanding of what exists and how we perceive that existence. Hume furthered this distinction by noting that we may form ideas based in sensory impressions- generating compound concepts based on the combination of sensory data (e.g., purple horse)- but that these concepts do not directly derive from perceptual experience. In postulating such, he distinguished between simple perceptions (e.g., color, form) and complex perceptions (e.g., the impression of an apple; Hume, 1748).

While early arguments of conceptualization focused largely on distinguishing between the subject (perceiver) and the object (thing perceived), affirming/denying the existence of the latter based on its 'accessibility' to and interaction with the former, important groundwork was set for some of the basic distinctions still relevant today. A concept as comprising a

subset of properties that may each have their own material grounding separate from the object itself as well as the multi-layered representation of a concept at the level of image, word, and meaning are quintessential elements of a definition of semantics. The taxonomic mapping of memory itself- the moving away from a purely individualized memory of past experience towards a fractionated system representing kinds of knowledge- led to the first formalization of what we now refer to as *semantic memory* in Quillian's 1966 doctoral thesis (for more detail, see Quillian, 1967). First referred to as a memory system for words and other verbal symbols, their meaning and referents and the relations between them, semantic memory was thought to encompass a highly-structured network of concepts, words, and images (Tulving, 1972). As such, it could be modeled through an implementation of discrete attributes that pertain to knowledge of an object and not merely an idiosyncratic experience of a specific object. Hume also implied this distinction between a concept *per* se and its instantiation in reference to the ideas we associate with a concept, be they general or particular; however, notably, he also posited that the imagining of an object in memory requires the internal activation of the same representation as the perceptual experience of that object. An irrefutable link between input from the external world, attributes fundamental to the generalized knowledge of an concept, and the internal activation resulting from the engagement with that concept thus has strong roots.

In the early 1970s, clinical neuropsychology shed light on several distinctions within the domain of semantics. A series of case studies appeared as breeding ground for the investigation of the newly-formalized division between episodic and semantic memory. Warrington (1975) described three patients of cerebral disease that presented with an

inability to recognize common objects, with an impairment extending beyond a perceptual or language deficit. While a division between the processing of a word stimulus and its associated meaning had appeared in the clinical literature nearly a century before- Lissauer (1890) invoking a Humean terminology for describing a deficit in "sensory impressions" versus "associative knowledge" in the organization of visual recognition- a comprehensive analysis of meaning had yet to be explored. Thus, the study of patients with various neurological disorders, ranging from herpes simplex virus encephalitis (HSVE) to ischemic lesion to what became known as semantic dementia, had offered important insight into the organization of the semantic system. This organization was first delineated in broad categorical terms. Warrington & Shallice (1984) described four HSVE patients that demonstrated a differential impairment in identifying nonliving entities compared with living entities and food. These results led them to postulating a theory of semantic memory based on particular properties relevant to each category. They argued that living entities are categorized more according to their sensory properties (e.g., color, shape) whereas nonliving entities rely more on functional properties (e.g., use and manipulability). In addition, they concluded that an entity might be *consistently* recognized from its visual representation but not necessarily from its verbal representation, arguing for the existence of modality-specific semantic subsystems.

The organization of semantic memory as described above- first, its categorical specificity, second, its division based on two main feature types, and third, it's modality-specific information processing- has been differentially interpreted and fit to theory. Theories of semantic memory can be divided into two basic groups- those that follow the neural

structure principle, which emphasizes representational constraints based on the internal neuroanatomical structure of the brain, versus the correlated structure principle, which assumes that conceptual knowledge is based on the statistical co-occurrence of object properties that renders certain categories more susceptible to deficit than others (for review, see Mahon & Caramazza, 2009). Fundamentally, theories of the former kind hold that the primary constraint on the organization of the semantic system is either by 1.) *modality*- specific modal subsystems differentially provide information relevant to each category; or 2.) *category*- categories with an evolutionary relevant history will serve the basis of organization and therefore damage to a category-specific domain will result in a loss of all information stored about that category. Of those theories that support feature-based organization of knowledge by subsystem, two even finer distinctions have been made. Lambon Ralph and colleagues (2016) have described two classes of theories that address the distribution of information across neural networks. The first view is the distributed-only view, which asserts that the entirety of the semantic network can be accounted for by the sensory-, motor-, and linguistic-processing regions through which information is both stored and accessed; the second is the distributed-plus-hub view, endorsed by the authors, and posits that, in addition to modality-specific processing regions, the flow of activation across all modalities converges at a common neuronal population that is activated irrespective of any single modality of input.

Support for the distributed-only view comes from differential performance of object retrieval based on the modality of input, selective neural activation relative to task and category, and patterns of semantic deficits that differ across categories (Borgo & Shallice,

2003; Warrington & Mccarthy, 1987; Warrington & Shallice, 1984). At the computational level, Rogers and colleagues (2001) generated a model with a weighted division between verbal and visual subunits that reflected performance patterns in semantic dementia with high accuracy. At the neural level, Martin and colleagues (1995) found that the color of an object is associated with bilateral activation in the ventral temporal cortex, whereas action-related information is association with activation in the middle temporal and frontal cortex. At the meta-analytic level, Binder and Desai (2011) analyzed 38 imaging studies employing language comprehension tasks and identified peak activation regions associated with the modality related to the type of categorical knowledge prompted by the task (e.g., auditory peaks occurred in superior temporal and temporoparietal regions whereas olfactory peaks were observed in the prepyriform cortex). Taken together, this evidence points to a semantic structure that does not emerge from categories adhering to certain boundaries as an organizing principle, but from categorical representations relying on different attribute types (Farah & Mcclelland, 1991; Warrington & Mccarthy, 1987).

The distributed-plus-hub view centrally addresses the cortical connections between representations and their convergence in an amodal hub (Patterson, Nestor, & Rogers, 2007). The utility of such a hub largely derives from computational models that emphasize the need for a system that generates *conceptual* similarities between objects when a reliance on *perceptual* similarities alone may lead to erroneous identification. According to this view, damage to the hub should produce a semantic impairment that is irrespective of the modality of input (e.g., objects, sounds, pictures) and the modality of output. One theory stemming from a position of unitary impairment is the Organized Unitary Content

Hypothesis (OUCH; (Alfonso Caramazza, Hillis, Rapp, & Romani, 1990), which proposes that categories are organized by intercorrelated features and that damage to any one feature domain relevant for that category would result in a ubiquitous deficit in retrieval of that category. In a later model, Caramazza and Shelton (1998) attempted to better account for the category-specific deficits witnessed in patient studies by highlighting the evolutionary significance of certain categories that gives rise to differential processing in anatomically distinct regions. Known as the Domain-Specific Knowledge Hypothesis (DSKH), it purports the dedication of distinct neural regions to processing different categories, one division among them being living versus nonliving entities. In such a model, each categorical neural domain is capable of receiving information from different sensory modalities, but implicitly attests to a more unitary representation that is not linked to the preferential activation of any single feature or modality. While neither theory specifically refers to amodal representations per se, subsequent elaborations have pointed to supramodal regions- namely the precuneus and posterior middle\inferior temporal gyri- in which amodal conceptual representations of objects are supported (Fairhall & Caramazza, 2013).

Another theory that has more explicitly postulated the necessity for a hub has seated it in the anterior temporal lobe (ATL; Patterson et al., 2007). One such theory, the hub-and-spoke model, while agreeing that the semantic network is widely distributed, also holds that the information flow from these distributed modality-specific regions should converge in the ATL, where a common set of neurons encodes the associations between these regions. Patterson et al. (2007) performed a conjunction analysis across 28 different

studies of semantic task performance, concluding that peak activation is continually witnessed in the ATL. This position is further enhanced by the profile of SD, which is characterized by bilateral ATL atrophy and in which global semantic impairment is observed (Lambon Ralph et al., 2007). SD-associated atrophy is in contrast with other patient lesion profiles that typically do not affect the ATL, and which could theoretically account for the category-specific deficits typically witnessed in the latter but not in the former. Recent work has attempted to unify evidence for global- versus selective-impairment through connectivity analysis and neuro-computational modeling, arguing that domain-general learning in the ATL along with both direct and indirect connectivity extending from this region to visual and action regions, could potentially reconcile diverging theories that have drawn from differing patterns of patient deficit (Chen, Ralph, & Rogers, 2017). However, the utility of such a hub that must account for all possible pairs of feature and task attributes to explain context-dependent effects remains a point of controversy.

Theories that follow the correlated structure principle assert that the co-occurrence of particular feature types that facilitate categorical knowledge and identification. According to Tyler and Moss' (2001) correlated feature-based model (Conceptual Structure Account; CSA), categories have different internal structures reflected through the interplay between feature correlations that are shared verses those distinct; highly correlated features support categorical knowledge as a whole whereas feature distinctiveness allows for the accurate discrimination between objects. The theory also assumes a division between living and nonliving entities, where shared features among living entities, versus distinctive features

of nonliving entities, are more highly correlated. By extension, Cree and McRae (2003) argue that the overlap in shared versus distinct features is what accounts for the category-specific deficits (living versus nonliving) that are observed in HSVE and other brain damaged patients. However, it is unclear as to the effect that feature similarity should render on the robustness of processing. On the one hand, high intercorrelation between features should create a more resilient system; on the other hand, it may also create higher interference. For instance, Humphreys and Forde (2001) make the claim that at the basic (specific) level, living entities share more common features than do nonliving entities (e.g. "dog" and "cat" share more features compared with "boat" and "airplane"). This greater similarity in features among living entities may account for the typically disproportionate deficit in living object identification among HSVE patients by creating a "crowding" effect resulting in low discriminability at the basic level.

Related work in considering the weighted influence given to certain features over others and the statistical relations among them has demonstrated the importance of context in semantic retrieval (Yee, Chrysikou, & L., 2013). While amodal models claim that semantic deficits are task invariant (for a conjunction analysis, see Bright, Moss, & Tyler, 2004), several studies have pointed to variation across semantic tasks that are indeed dependent on context. Devlin et al. (2002) conducted a multifactorial analysis with category type (e.g., animals versus tools), stimulus type (e.g., words versus pictures), and task type (e.g., perceptual decision versus semantic decision) and found differential activation across tasks as well as stimuli. For instance, the percentage of regional cerebral blood flow change varied significantly between perceptual and phonological tasks in the

right and left anterior temporal poles. Moreover, at the categorical level, tool naming specifically activated the left posterior middle temporal gyrus in all tasks except those involving phonological or visual inputs and outputs. Although tool use has typically been associated with activation in the inferior parietal cortex (Chao & Martin, 2000), the crucial aspect is the interaction between category-specificity and task-relevant constraints. As predicted by sensorimotor-based theories, damage to a region responsible for the encoding of modality-specific information (e.g., auditory, visual, or motor) will affect retrieval of information about an object that necessitates that modality for its processing (Bonner & Grossman, 2012).

While an exhaustive list of theory is not herein considered, the selective literature does reflect the motivational impetus for the current doctoral work. The interaction between category and feature type is at the core of the following chapters. Beginning with the broad categorical dissociation between living and nonliving entities inspired by early case studies, a finer-grained distinction within the living category is considered- namely, that of fruits/vegetables. Furthermore, the reliance of a category on specific attributes for its representation at the basic level of processing- as conceptual "primitives" (Martin, 2016)- is investigated for fruits/vegetables and utensils (tools). The category of fruits/vegetables has been difficult to reliably map onto a living/nonliving dichotomy given diverging patterns of deficit witnessed in patient studies (Blundo et al., 2006; Hillis & Caramazza, 1991; Warrington & Mccarthy, 1987). However, irrespective of the organizing principle of semantic memory favoring a feature-based or category-based account, fruits/vegetables should occupy a "privileged status" in the semantic system and demonstrate properties that

1.) render it susceptible to changes in those features, and/or 2.) allow for a dedicated neural network to its processing.

It is important to note that the current body of work only deals with a restricted subset of the properties that fall into the general division of sensory and functional properties- namely, color and orientation, respectively- as these are the features that have garnered considerable attention in the conceptual division between living/nonliving entities. The sensory properties (e.g., color, shape, texture) of an object are considered distinct from 'perceptual' knowledge of an object, which can refer to either its visual characteristics (as it is intended herein) or how information about an object is processed through perceptual channels that may or may not be different from the visual modality (Capitani et al., 2003). The use of 'modal' versus 'amodal' representations will also be used throughout the text. In some interpretations, amodal refers to conceptual representations that do not necessitate the activation of specific modal (e.g., visual, motor, etc.) regions for their processing and can be accessed independently of the modality of input (e.g., reading the word 'cat' or seeing a picture of a 'cat' would activate the same conceptual information). In other interpretations, amodal may reflect a processing region, such as a hub, that may receive convergent input from modal subsystems differentially active for specific categories, but where it itself is not preferentially responsive to any single modality of input. However, it is implicated as one central node in a web of connectivity between modal subsystems that abstracts from modality-specific activations. Conversely, modality-specific processing strictly refers to the activation of perceptual modalities in the processing of specific categories that differentially depend on information from that modality for its

conceptualization. As has been stated in the GRAPES model (Martin, 2016), this does not necessarily imply that the exact low-level regions responsible for object-associated properties like color and shape should be active in the representation of an object that relies on that property for its conceptualization, but nearby downstream regions situated within that perceptual modality is where information regarding that property should, in principle, be stored and retrieved.

In the subsequent chapters, the automatic processing of specific features- namely *color* and *orientation* information- for both fruits/vegetables and tools is explored through a lexical decision identity priming paradigm (chapter 1) and the neural evidence associated with this processing (chapter 2). Finally, chapter 3 considers a network for the processing of fruits/vegetables, as has already been established for other categories in the literature (i.e., faces, places, and tools).

CHAPTER 1

Introduction

Broad semantic distinctions

One important issue to the study of cognition is how the brain processes conceptual representations. According to modal theories of semantic processing, conceptual knowledge is processed in specialized sensory, motor, and linguistic regions through which information is both stored and accessed, whereas amodal theories posit a unitary "hub" to which activation across all modalities converges (for review, see Patterson et al., 2007). Much support for modal theories has come from patient studies that have demonstrated category-specific deficits for living, nonliving, and food entities, postulating a categorical organization based on specific features relevant to each category- that is, living entities rely on sensory properties (e.g., color, shape) and nonliving entities on functional properties (e.g., use and manipulability) for their classification (Borgo & Shallice, 2003; Warrington & Shallice, 1984). Indeed, neurophysiological evidence for categorical processing in dedicated brain regions has been shown, with lateral portions of the fusiform more active for animals (e.g., living, or natural) as compared to manmade tools (e.g., nonliving, or artificial; Chao, Haxby, & Martin, 1999) and distinct feature processing regions linked to color information (i.e., ventral temporal cortex) versus action-related information (i.e., middle temporal and frontal cortex; Martin et al., 1995). However, while the distinction between animals and manmade tools as two instances of natural and artificial entities, respectively, has received considerable attention, how food entities fit into this broad categorical framework has been largely under investigated.

Food as dissociable category

Capitani and colleagues (2003) provided an exhaustive review of patient profiles including those demonstrating a selective deficit for identifying animals while showing spared processing of food entities (Caramazza & Shelton, 1998) and vice versa (Hart, Berndt, & Caramazza, 1985), with a similarly inconsistent pattern between tools and food. One reason for the inability to map food onto the living/nonliving dichotomy could be due to its special evolutionary status, as predicted by the Domain-Specific Knowledge Hypothesis (DSKH; Mahon & Caramazza, 2011), reflecting an internal organization of semantics based on category type, with each categorical domain capable of receiving information from different sensory modalities. However, another potential reason could be that the category of food is composed of finer distinctions that have not been systematically considered; stimuli spanning from liquids, to fruits/vegetables, to manufactured food items may render featural overlap with both living and nonliving entities (Capitani et al., 2003). Considering this confound, the current study considers only fruits/vegetables as representative instances of the natural category, as a biological definition would suggest.

Color diagnosticity and natural entities

Some evidence has shown that natural entities- fruits/vegetables among these- rely largely on sensory information (e.g., color) for their classification. In a study by Tanaka and Presnell (1999), participants were presented with an object classification task in which both grayscale and color images were paired with a matching or nonmatching word and had to indicate if there was a match by button press. They found that reaction time performance varied according to how color diagnostic the object was previously rated to

be- that is, objects for which a color was listed as an integral feature to its concept showed a greater facilitation of reaction time when the word matched the color version. Similarly, Rossion and Pourtois (2004) demonstrated that fruits/vegetables show a particularly strong advantage of correct color presentation, with the reasoning that color is particularly informative given their structurally similar shape.

However, there have been equivocal findings as to the importance of color in object recognition. Biederman and Ju (1988) found that the inclusion of color information did not facilitate performance for neither color diagnostic nor color nondiagnostic objects. Furthermore, in a recent study by Scorolli and Borghi (2015), it was shown that when fruits were distorted in both shape and color, shape manipulations more negatively impacted classification. Therefore, the relative importance of color and shape on conceptual processing of natural entities has been met with mixed results.

Orientation and artificial entities

Artificial entities, namely manmade tools, have been considered, by some accounts, to rely to a large extent on functional information (e.g., manipulability). For instance, in an orientation classification task, Tucker and Ellis (1998) presented participants with photos of manipulable objects with a graspable feature (e.g., handle) for which they had to categorize as inverted or upright. Objects were presented at a graspable orientation that was either compatible or incompatible with the response hand, with quicker reaction times found for objects spatially aligned to the responding hand (i.e., affordance effect; Gibson, 1977). Such sensitivity to affordance has also been observed in tasks of priming in which

prior exposure to an oriented line that is congruent with the axis of graspability of a subsequently presented object has facilitated orientation judgments (Chainay, Naouri, & Pavec, 2011). These results have supported the notion of automatically-activated motor representations even in the mere viewing of that object without action execution (Grèzes, Armony, Rowe, & Passingham, 2003). However, this automaticity of processing has been challenged by a recent in study in which Yu and colleagues (2014) were only able to replicate the findings of Tucker and Ellis when participants were explicitly asked to imagine interacting with the pictured object. This suggests that relevant motor regions may be activated only under specific circumstances such as goal-directed behavior.

Taken together, the extent to which natural and nonliving entities rely on sensory versus functional features, respectively, for their processing is still under debate and is the question addressed by the current study.

Semantic priming

One useful way to investigate categorical processing has been via the method of priming. Several studies have found a facilitation of processing, manifested as an decrease in reaction time performance, to a target word when it is preceded by a semantically-related or identical prime word (de Wit & Kinoshita, 2014; Kinoshita & Norris, 2012; Neely, 1991; Perea & Rosa, 2002). Although such an effect has more frequently been tested in unimodal word-word priming, some studies have also demonstrated a crossmodal picture-word priming effect that may, furthermore, be differentially impacted based on category type (Kahlaoui, Baccino, Joanette, & Magnie, 2007). The aim of the current study is to investigate the effect of sensory and functional features on categorical processing of

natural and artificial entities using a cross-modal lexical decision task. In such a task, participants are first presented with an image of an object, followed by a string of letters and have to decide if the string represents a word or nonword. The premise is that on word trials, when the word is preceded by a semantically-related prime (in the current experiment, 'semantic' priming is achieved by identity priming), participants will be quicker to identify a word target. Herein we manipulate prime-target relatedness by modifying features of the prime image that should be highly relevant for categorical processing of the target word; we refer to the achieved effect within a semantic priming framework, due to the potential reduction in relatedness induced by the manipulation. That is, we predict that if natural entities do indeed rely on sensory features for their categorization and artificial entities on functional properties, then a modification to either one of these features will reduce the semantic prime-target relatedness and thus diminish the priming effect. If such features are salient to conceptual processing, an interaction between category and feature type should be observed even in the case of automatic priming (Dell'Acqua & Grainger, 1999) and in cross-modal domains (Kircher, Sass, & Sachs, 2009).

Methods

Participants. A total of 60 healthy right-handed, native-Italian speakers with normal or corrected-to-normal vision participated in the experiment (age range: 18-34 years). Participants were recruited via an advertisement posted on a dedicated social-networking site, and were monetarily compensated for their participation. After data inspection, three participants were eliminated due to poor performance (see Results section for detailed

explanation), with 57 participants (29 female) remaining in the final analysis (age: M = 23.67; SD = 3.32). All participants were naive to the purpose of the experiment and provided informed written consent. The experiment was part of a program that has been approved by the ethics committee of SISSA.

Materials. Forty–two Italian words served as critical target stimuli for the experiment. Twenty–one of them represent natural objects (fruits/vegetables ; e.g., *pomodoro*, tomato) and twenty–one represent tools (kitchen utensils; e.g., *forchetta,* fork). The main lexical features of these 42 words are illustrated in Table 1. Frequency was considered according to zipf, which is a logarithmic scale that considers the size of the corpus in the frequency distribution (van Heuven, Mandera, Keuleers, & Brysbaert, 2014).

Table 1. *Lexical features for each category.*

Lexical features	**Natural**		**Artificial**	
	Mean	*SD*	*Mean*	*SD*
Frequency (zipf scale)	3.11	0.55	3.07	0.72
Letter length	7.24	1.82	8.1	2.11
Coltheart's N	12.43	19.8	7.57	6.53
Old20	1.8	0.58	1.88	0.74

Each target word was associated with three different prime images, representing the corresponding object: (i) in its canonical color and position[1] (identity prime); (ii) with a clearly non–standard color (color modified prime); (iii) with a clearly non–standard

[1] In the case of objects without a clear canonical base position (e.g., knife; see (Vannucci & Viggiano, 2000), the original image was chosen to be that with maximum affordability for a right–hand grasp (Tucker & Ellis, 1998).

position (orientation–modified prime). Identity primes were all taken from the FRIDa database (Foroni, Pergola, Argiris, & Rumiati, 2013).

For the orientation modification, images were rotated 180 degrees in the counterclockwise direction; in the case of natural and base artificial objects, this created a vertical inversion, while for no–base artificial objects, this rendered a maximum incompatibility with affordance of right–handed graspability.

For the color modification, images were converted to CIELab, which nonlinearly compresses an RGB color image into a three–dimensional coordinate space with the position on one axis representing the red-green opponent channel (a), another the yellow–blue opponent channel (b), and the third the lightness of color, which is the cube root of the relative luminance (L; Hoffmann, 2003). The advantage of using such a color space is that the lightness contrast can be manipulated independent of a color modification. Furthermore, transformations of images that are high in gray content respond well to manipulations in this color space, meaning that more drastic changes can be achieved as compared to a uni–coordinate modification of hue in the HSL or HSV color space. This was particularly useful for the artificial category, which contained a high number of objects whose principle color was gray. Modifications to both natural and artificial objects were achieved using a custom–written MATLAB® code and made by a fixed proportional change in the a– and b–channel value coefficients, the position of each pixel for either axis multiplied by .8 and .2, respectively. This created a purple–blue effect, which rendered a color most naturalistically improbable for the natural category in particular, given that in

the predominantly gray artificial category, any color modification was comparatively equidistant from the original image. Examples of these prime images are given in Figure 1.

Identity prime images were matched between natural objects and tools for brightness, spatial frequency, and size in addition to evaluative ratings of discriminability and familiarity, which were based on a 100-point scale. These ratings were obtained from the normative ratings of the FRIDa database (values of all features are presented in Table 2).

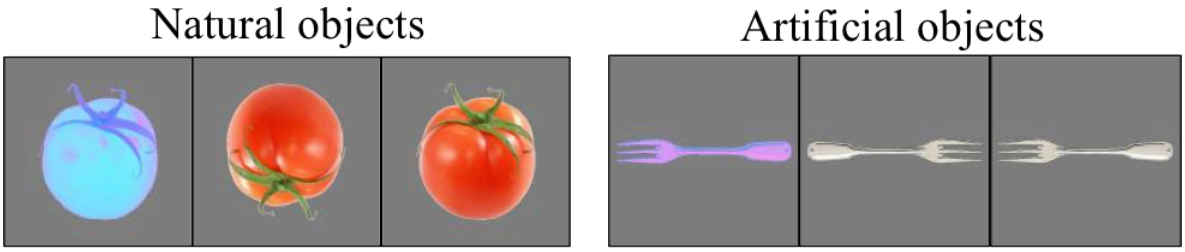
Table 2. *Visual properties and evaluative ratings of stimuli for each category*

Condition	**Natural**		**Artificial**	
	Mean	*SD*	*Mean*	*SD*
Brightness	134.12	10.49	133.77	9.86
Spatial frequency	0.0052	0.0022	0.0059	0.0013
Size	0.0006	0.0023	0.0007	0.0032
Discriminability	7.61	18.46	8.13	15
Familiarity	58.3	28.9	57.15	29.11

To compute brightness, images were converted to grayscale and the average brightness extracted. To compute size, objects were isolated using a layer mask in an online image editing application (https://pixlr.com/). Pixels representing the object were converted to black, the background was converted to white, and the ratio between the two was calculated. Spatial frequency was calculated by employing a bi-dimensional fast Fourier transform, which converts the image represented as an array of brightness values to its unique representation in the spatial frequency domain. After transformation, individual pixels represent the power of specific spatial frequencies in a given direction (Foroni et al.,

2013). Values for each feature were obtained using custom-written MATLAB® codes (Mathworks, Natick, Massachussets, USA). Because color and orientation–modified images underwent the exactly same pipeline, this matching also applies to them.

Figure 1. *Example of prime images for both natural and artificial categories. Left image for each category depicts a color modification, middle image an orientation modification, and right image canonical color and position.*



The assignment of each word target to the three priming conditions was counterbalanced over participants, so that all participants received primes from each condition, but saw each target only once.

For the purpose of the lexical decisions task, 42 nonwords were created as further target stimuli. They were created from real words by either vowel inversion or single consonant substitution (e.g., *pentalo* from the Italian word *pentola*, pot). In order to avoid that participants could carry out the task based on stimuli surface features, words and nonwords were matched for length in letters (Words: *M*- 7.67*, SD*- 2.02; Nonwords: *M*- 7.55*, SD*- 1.75) and orthographic neighbourhood size (as measured by OLD20; Words: *M*- 1.84, *SD*- 0.658; Nonwords: *M*- 1.9, *SD*- 0.686). These targets were also associated with prime images, similarly to the word–target stimuli. In this way, both word and nonword targets were semantically related to prime images (e.g., prime image of PENTOLA

succeded by target nonword PENTALO), thus reflecting the same prime-target relatedness proportion. The relatedness proportion between prime-target pairs is considered to influence the size of the semantic priming effect as participants can generate expectancies regarding the identity of the target from semantic information of the prime (De Wit & Kinoshita, 2015; Neely, 1977). In the current study, the relatedness proportion between prime and target was 1 for both words and nonwords, meaning that participants could not use a retrospective matching strategy (Neely et al., 1989) to identify words differentially from nonwords based on a semantic relationship that only target words share with the prime. The words from which the nonwords derived were matched in frequency to the word trials ($t(82) = .115$, $p = .909$). However, nonword-target stimuli were randomly paired with only one image (e.g., normal, color, or orientation) and were not subjected to rotation.

Images were displayed within a 450–pixel square, against a gray background. All letter strings were presented in size 36 Courier New Font, and displayed in white on the same gray background.

To avoid repetition effects, three groups of participants were used, each being presented with a subset of the stimuli (only one condition of each prime object). That is, target strings were paired with only one prime condition that was rotated across the three groups.

Procedure. Participants were tested in a dimly lit room. They were seated in front of a computer screen (at a distance of approximately 60 cm), and instructed to decide whether

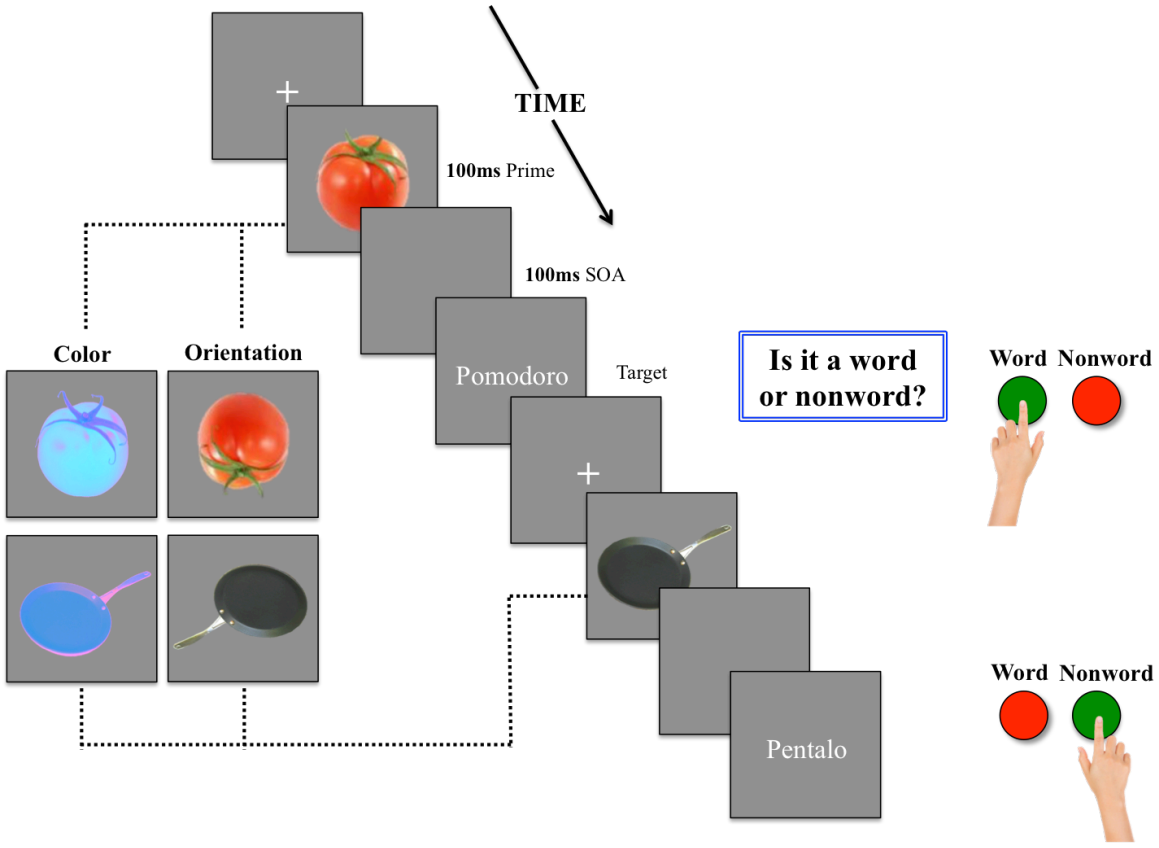
or not the letter strings appearing on the screen represented existing Italian words. On each trial, a fixation cross (500ms duration) was followed by the presentation of the prime image (100ms duration) image, which was followed by a blank screen (100ms duration) and then by the target string of letters. Participants were asked to respond by key press to the question "Is it a word or a nonword?" (for a schematic, see Figure 2) as quickly and accurately as possible. Keys associated with word and nonword trials were counterbalanced across participants.

Participants were told that the letter strings would be preceded by a fixation cross, but no mention was made of the presence of the prime images. They were only informed that the current study wished to investigate how well they could identify words and nonwords. Participants were given six practice trials to familiarize themselves with the task, in addition to the first trial being considered as a practice trial. At the end of the experiment, participants were asked if they 1.) understood that the target strings were preceded by an image and if so, 2.) if they thought that there was any relationship between the prime and the target. Participants were generally aware of the presence of the prime and that it represented (in some cases) the subsequent target string. However, no analysis was performed on this data. Participants were then debriefed as to the scope of the experiment and requested not to share the information with others who may partake in the experiment.

Overall, the experiment included 84 trials (i.e., ~7 trials per condition), for a total duration of about 6 minutes, with the first trial being omitted as practice. Stimuli were presented

using E-Prime 2.0 Professional (Psychology Software Tools, Sharpsburg, PA) on a 48–cm diagonal monitor (resolution: 1280 x 1024 pixels; aspect ratio 4:3; refresh rate: 75Hz).

Figure 2. Schematic of trials of normal condition with color and orientation modification conditions shown to the left. Participants were asked to respond by key press to the question "Is it a word or nonword?" Target strings remained on the screen for 3000ms or until key press.



Analysis. Data were analyzed using mixed–effect modeling as implemented in the *R* package *lme4* (Bates, Maechler, & Dai, 2009). The dependent variable was response time, with a Q-Q plot confirming the non-normal distribution of the RT data. Therefore, data

was inverse-transformed (i.e., 1/reaction time) to achieve normality, the inverse approach typically considered to be the optimal transformation for positively-skewed RT data (Baayen & Milin, 2010).

Fixed factors were target Category (natural object vs. tools), prime Condition (normal vs. color-modified vs. orientation-modified image) and their interaction. This defines the core structure of the experimental design. Participants and target words were also specified as random intercepts, thus taking into consideration the theoretically uninteresting variation introduced into the data by these factors (individual participants may be fast or slow overall, and individual target words may be difficult or easy, independently of any experimental manipulation). Robustness to outliers of the model estimates was checked with model criticism as advocated by Baayen, Davidson, and Bates (2008; i.e., models were refitted after removing those data points whose standardized residual error was higher than 2.5 and effects were considered significant only if they resisted this procedure). P-values were computed adopting the Satterthwaite approximation for degrees of freedom (Satterthwaite, 1946) as implemented in the lmerTest R package (Kuznetsova, Christensen, & Brockhoff, 2013). This package, in addition to *ggplot2* (Wickham, 2009), *reshape* (Wickham, 2007), and *visreg* (Breheny & Burchett, 2013), was extensively used as part of the R system for statistical computing (Ver. 2.8.1; R Development Core Team, 2013).

Results

Three participants were excluded from the analyses based on having exceeded three standard deviations in either reaction time (1 participant) or accuracy (2 participants) performance. Furthermore, RTs were first visually inspected and accordingly trimmed for outliers that were implausibly generated by a psychological process related to the task (e.g., inattentiveness), which resulted in the removal of only a single data point. One word was also eliminated from the analysis due to an accuracy of less than 85%. This left 4739 data points in the final analysis, of which 2254 were word trials. The overall accuracy rate for the task was 94.45%.

We first compared RTs of words versus nonwords, which a significant difference in performance ($t_{(56)} = -10.88$, $p < .001$), with words being more quickly identified than nonwords (Word: *Mean* = 732.6 ms, *SD* = 257.46 ms; Nonword: *Mean* = 836.62, *SD* = 268.27). Shorter RTs for words is an expected and well-documented finding in the literature and largely explained by the "automaticity hypothesis", which posits the existence of a mental lexicon (Schvaneveldt & Meyer, 1973). As the question of interest concerned the degree to which feature modifications of a prime influence semantic processing of a target concept, nonword trials were discarded and further analysis performed only on word targets.

For all word trials, Condition (normal, color-modified, orientation-modified) and category (natural and artificial) were first entered in a model as fixed factors. Subsequent models were hierarchically constructed with the inclusion of participant and word as random

factors, which took into consideration the individual variation introduced into the data by these factors each representing only one sample drawn from a conceptually larger population. The final model was confirmed as the simplest with maximum explained variance by the likelihood ratio test, as proposed by (Pinheiro & Bates, 2000). Akaike Information Criterion (AIC), which measures the relative quality of a statistical model with respect to goodness of fit and least complexity, penalizing for number of included parameters (Akaike, 1973), provided this index for model choice. Input data for each model and values of the model comparisons can be found in Table 3. The lowest AIC with p-value significance denotes the preferred model.

Table 3. *Upper panel: Model formulas for the three different models and factor specifications. The first model contains only fixed effects whereas the second and third contain the random effects of participant and participant + word, respectively. The response variable (invRT) is the inverse RT. The format (1|"explanatory variable") considers the random intercepts of the explanatory variable, allowing them to vary as a function of the levels of that variable. Lower panel: Model comparison for the three models. The deviance score (AIC) is smaller for M2 (inclusion of both participant and word as random factors).*

Model	Formula
M0	invRT~Condition*Category
M1	invRT~Condition*Category + (1|Participant)
M2	invRT~Condition*Category + (1|Participant) + (1|Word)

Model	Df	AIC	BIC	logLik	Chisq	Chi Df	Pr(> Chisq)
M0	7	-28639	-28599	14327			
M1	8	-29366	-29320	14691	728.91	1	< .001
M2	9	-30051	-30000	15034	686.81	1	< .001

Statistical modeling revealed a significant effect of target Category [$F(1, 38.93) = 7.7$, $p = .008$], prime Condition [$F(2, 2842.39) = 6.86$, $p = .001$], and, most importantly, their

interaction [F(2, 2842.31) = 4.47, p = .01]. Mean response times and standard deviations for the six conditions are illustrated in Table 4.

Table 4. *Raw RT means for condition x category.*

Condition	**Natural**		**Artificial**	
	Mean	*SD*	*Mean*	*SD*
Normal	672.67	221.06	759.79	258.83
Color	705.41	230.66	779.24	276.92
Orientation	684.98	235.51	804.28	292.36

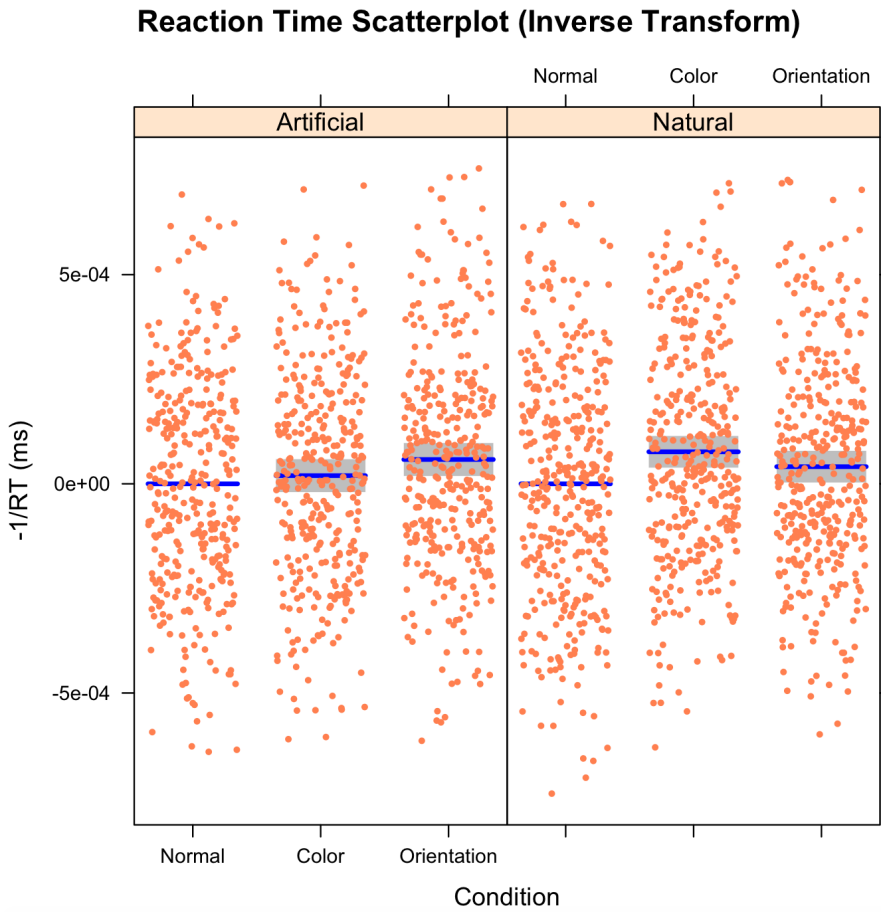
To explore the interaction, the best model was divided by category into two separate models and atypical outliers were removed (Baayen & Milin, 2010), employing a 2.5 SD of the residual errors as criterion as has previously been done (Marelli, Amenta, Morone, & Crepaldi, 2013). Given that the comparison of interest was between color and orientation modifications in each category, parameter estimates and t-statistics for the fixed effects of the category-specific models are reported with respect to the relevant condition in Table 5.

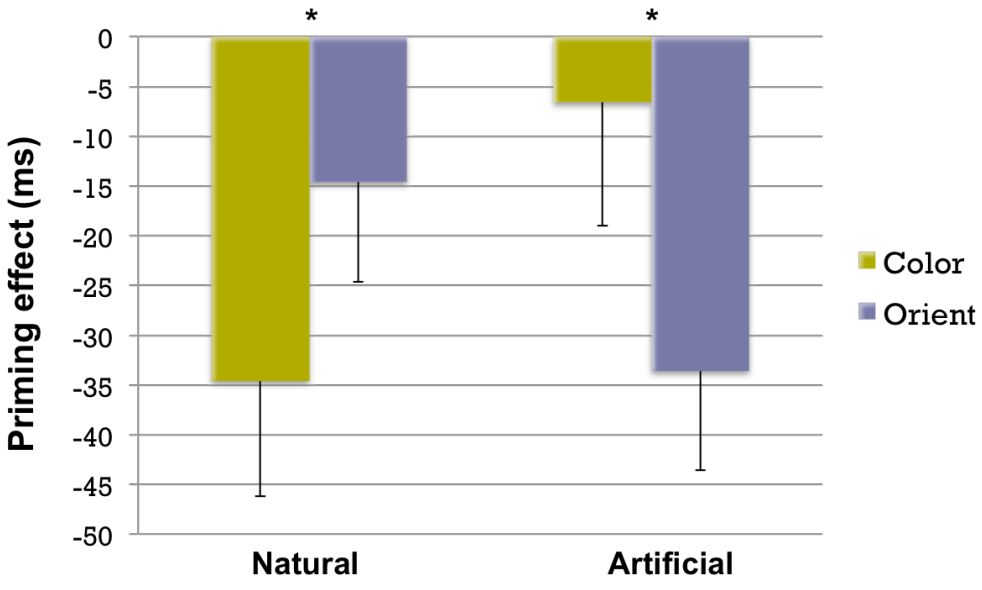
Table 5. *Parameter estimates and t-statistics of fixed effects divided by category. For the natural category, the model was releveled for a comparison to the color condition, whereas for the artificial category, the model was releveled to the orientation condition.*

Fixed factors	**Estimate (b)**	**T-stat**	**Pr(>|t|)**
NATURAL			
Color vs.			
Normal	-7.458e-05	-3.87	<.001
Orientation	-4.126e-05	-2.12	0.034
ARTIFICIAL			
Orientation vs.			
Normal	-5.689e-05	-2.88	.005
Color	-3.962e-05	-2	.045

There was a significant difference in the priming effects of color- and orientation-modified primes with respect to the category. For words depicting natural entities, color-modified primes yielded significantly less priming than orientation-modified primes; for words depicting artificial entities, orientation-modified primes yielded marginally significantly less priming than color-modified primes. Importantly, this effect was in the direction of the hypothesis, as is exemplified by Figure 3.

Figure 3. *Upper panel: Scatterplot of the interaction with the normal condition scaled to 0. Blue lines indicate means and gray shading standard deviation. Lower panel: Priming effect for color and orientation, divided by category, after subtracting the normal condition. Negative RT reflects reduction in priming for the manipulation conditions relative to the normal condition.*


Reaction Time Scatterplot (Inverse Transform)
Normal
Color
Orientation
Artificial
Natural
5e-04
0e+00
-5e-04
-1/RT (ms)
Normal
Color
Orientation
Condition


*
*
0
-5
-10
-15
-20
-25
-30
-35
-40
-45
-50
Priming effect (ms)
Natural
Artificial
Color
Orient

Reaction times were also binned into quartiles to explore the effect across the distribution. F-statistics and p-values for the effect of condition across quartiles, divided by category, is provided in table 6. An interesting finding is that, for the natural category, a visualization of the data revealed a similar pattern of performance across all response time intervals. However, for the artificial category, the main effect of condition emerged at later time intervals, representing a distributional shift. Such a shift in RT distribution could potentially be attributable to retrospective retrieval processes, where the target is semantically matched to the prime (Yap, Balota, & Tan, 2013). An analysis of the exgaussian distribution, which is the convolution of a Gaussian and exponential distribution that considers such distributional shifts, was also performed. Mu, sigma, and tau parameters were extracted, corresponding to the mode and standard deviation of the Gaussian and the approximated exponential function, respectively. A significant effect of category was found, [$F(1, 280.05) = 17.86$, $p < .001$], with a higher tau in the artificial ($M = 149.66$; $SD = 92.8$) than the natural ($M = 114.6$; $SD = 77$) condition (see Table 6 for significance values). This finding suggests that the effect of a prime modification on the artificial category was expressed at later time points as compared to the natural category.

Table 6. *F-statistics for anova of models divided by category and quartile.*

Quartile	**Natural**		**Artificial**	
	F-value	*Pr(>F)*	*F-value*	*Pr(>F)*
Q1	13.52	<.001	1.59	.206
Q2	15.46	<.001	4.42	.02
Q3	14.87	<.001	12.7	<.001
Q4	1.45	.235	5.69	.004

Discussion

In the current study, we used a lexical decision task of identity priming to test the hypothesis that natural and artificial entities rely on different properties for their semantic processing. We have shown that indeed, the processing of natural entities is more sensitive to modifications of a sensory property (i.e., color), while that of artificial entities is more sensitive to modifications of a functional property (i.e., orientation). Moreover, this effect is present at the cross-modal level.

We chose the method of priming at a short SOA in order to tap into fast, automatic semantic processing (Neely, 1991). Even at an SOA of 100ms, prime images could activate the semantic concept leading to a facilitation of processing at the lexical level. Previous studies have also supported automatic cross-modal priming of both natural and artificial entities (Dell'Acqua & Grainger, 1999; Kircher et al., 2009). This facilitation of processing at short SOAs suggests a potential overlap of visual- and lexico-semantic domains, with a transfer of information between the two that is reflective of semantic processing. It can be said that the priming effect that we report truly represents access at the conceptual level also given an equal prime-target relatedness proportion for both word and nonword trials. This relatedness proportion has been considered a problematic aspect of most prior priming studies, where nonword targets are usually not paired with primes related to a word that the nonword resembles (as in, e.g., BANANA – APFLE; de Wit & Kinoshita, 2015). We wished to address this potential confound to add clearer evidence to the literature of any effect that may have emerged.

Regarding the effect of feature modification differentially across categories, Thompson-Schill and Gabrieli (1999) used a semantic classification task at study and test to measure implicit conceptual memory by manipulating the type of attribute- visual or functional- to which participants had to access about the stimulus at each stage. They found an advantage for same-attribute priming at study and test, suggesting that there may be separate semantic representations for visual and functional knowledge. We have herein shown that the presentation of sensory- or functionally-relevant features can differentially enhance or detract from the priming effect depending on the type of category, which is evidence more in favor of the sensory-functional hypothesis first proposed by Warrington and Shallice (1984). According to said theory, conceptual knowledge is organized into modality-specific subsystems, with sensory knowledge being relevant for the categorization of natural entities and functional knowledge for that of artificial entities. Having used fruits/vegetables as instances of the natural category, we have demonstrated that this division also extends to the domain of fruits/vegetables. Our findings are somewhat at odds with those of Scorolli and Borghi (2015), who found that shape processing was more important than color to the identification of fruits. However, in their study, they employed both a categorization and manipulation task, for which, in the former, shape distortions had a greater negative impact on reaction time compared to color, while in the latter, there was no difference. Arguably, the categorization task did not access semantic knowledge per se', but feature distortions could have differentially impacted more low-level visual processing. Although explicit ratings indicated that participants judged the effect of distortions of both features equally, task performance suggests that different routes of semantic processing may have been induced by task type. It is also important to note that

both animals and fruits- two instances of the natural category- were used in their study, yielding diverging results depending on feature modification. While our results support a sensory-functional distinction based on category type, much in line with Warrington and Shallice's (1984) hypothesis, a review of the patient literature on categorical deficits has shown that knowledge for fruits/vegetables and animals can be dissociably impaired (Capitani et al., 2003). How members of the natural type dissociate is still under debate.

We also found an advantage for natural entities over artificial entities in identifying word targets. Given that words were matched for frequency and letter count, this finding cannot be attributable to low-level lexical effects. This finding is been met with mixed results in the literature, some authors having reported quicker reaction times for natural entities (Dell'Acqua & Grainger, 1999) while others for artificial entities (Kahlaoui et al., 2007). One interpretation for the advantage that we find could be due to fruits/vegetables being evolutionarily significant and therefore occupying a distinct anatomical region that receives information from different sensory modalities (DSKH; Caramazza & Shelton, 1998). However, given the graded priming effect of feature modification (e.g., for fruits/vegetables, a reduction of priming most sensitive to a modification of color, followed by orientation, followed by the canonical representation), it is unlikely that this hypothesis alone can explain our findings, given the lack of preferential activation of any single feature that a unitary representation entails.

The artificial category of tools also demonstrated a graded effect of priming, moreover in the absence of overt instructions to compare prime and target, contrary to what some

previous studies have suggested (Bajo, 1988; Yu et al., 2014). Our findings are in line with the previous literature demonstrating automatically-activated orientation-priming effects for objects presented in the canonically graspable position (Chainay et al., 2011; Grèzes et al., 2003). We have also observed that the feature modifications in the artificial category appear to render an effect on semantic processing more so at later time points in the reaction time distribution. Given that visual information may occur at earlier stages of processing than functional information (D'Arcais, Schreuder, & Glazenborg, 1985), this effect may be due to the time course of functional information processing. Furthermore, the representation of functional information in semantic memory may reflect a more complex hierarchical structure that leads to differences in processing time; for instance, tools versus nonmanipulable entities have been speculated to differentially activate dorsal and ventral streams, respectively (Almeida, Mahon, Nakayama, & Caramazza, 2008).

The fact that a graded priming effect was observed for both categories also reinforces the view that feature-based constraints limit processing at the conceptual level. While color is most integral to the processing of fruits/vegetables and orientation to the processing of tools, there were also significant reductions in priming for each of the modified conditions with respect to the normal condition. One interpretation could be that indeed, while a certain feature may be of critical importance to a particular category, other features may also play a role in the conceptual representation. Given that our task employed two feature modifications in addition to a normal condition, a task-induced access of other stored feature representations could have been possible. Fruits/vegetables can also be considered as graspable entities and invoke motor affordances in the categorization process, although

such an effect has been observed for overt responses to graspability (Netelenbos and Gonzalez, 2015) and not as an automatic activation of action affordance at the conceptual level as is shown here. Similarly, some objects within the artificial category of utensils could also possess a degree of color diagnosticity (e.g., forks, knives, spoon, etc. being canonically silver); indeed, some research has demonstrated a facilitation of object recognition for artificial entities that are typically associated with a particular color (Therriault, Yaxley, & Zwaan, 2009).

We have herein demonstrated that categories rely on different features for their semantic categorization and moreover, this is reflected as automatic conceptual processing. Given the graded priming effect as an interaction between feature manipulation and category, in addition to the reaction time advantage for fruits/vegetables, it would be interesting to investigate the time course of semantic processing at the more refined neural level, by employing EEG to our paradigm. Some studies have already shown different time courses of peak activation depending on category type (Papagno, Martello, & Mattavelli, 2013) as well as graded peak activity based on prime-target similarity (Geukes et al., 2013). However, a direct comparison between feature processing and category type, to the best of our knowledge, has yet to be explored.

CHAPTER 2

Introduction

The nature of category-specific effects in semantic processing is a fundamental issue that is still heavily under debate. Largely informed by neuropsychological studies with brain-damaged patients (for a review, see Capitani, Laiacona, Mahon, & Caramazza, 2003), selective impairment in specific categories of objects has broadly distinguished between natural and artificial (manmade) entities with several theories emerging as to their structural organization in the brain. Whether conceptual representations are distributed over modality-specific systems or contained in modality-independent regions has led to differing opinion as to the reliance of certain categories on specific features for their processing (for reviews, see Mahon & Caramazza, 2009, Martin, 2007).

Theories aiming to explain category-specific deficits fall into two general groups: those that follow a neural structure principle, claiming that dissociable neural substrates are differentially involved in representing categories, and those that ascribe to a correlated structure principle, which posits that the correlation between the properties of objects differ across categories, but that the system itself reflects no structural division by category (Mahon & Caramazza, 2009). One prominent theory belonging to the former is the sensory/functional theory of semantics (or a later variant being the sensory-motor model; Martin, Ungerleider, & Haxby, 2000) whereby concepts are *grounded* in the sensory and functional subsystems that are relevant to their processing. Specifically, natural entities critically depending on sensory knowledge for their classification and artificial entities on functional properties could account for the patterns of deficits witnessed in early

neuropsychological literature (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). Neurophysiological evidence has not only pointed to distinct neural correlates for the natural versus artificial entities (Chao et al., 1999; Perani et al., 1995) but to an interaction between category and feature type; objects and their relevant sensory or functional attributes have shown to activate similar neural regions (Martin, Wiggs, Ungerleider, & Haxby, 1996; Noppeney, Price, Penny, & Friston, 2006; Tyler et al., 2003). The current study focuses on the relationship between sensory and functional knowledge as they pertain to instances of natural and artificial categories, respectively.

Of the sensory attributes theoretically associated with natural entities, color has garnered particular attention. An early PET study by Martin and colleagues (1995) found that the generation of a color typical to an object compared with an action associated with it led to selective activation of a region of the ventral temporal lobe slightly anterior to the area involved in color perception. Simmons and colleagues (2007) later demonstrated a direct overlap in the fusiform gyrus between color perception and object-associated color knowledge. One important point here is that although a grounded-cognition framework posits that an object relying on color, for instance, should activate the perceptual subsystem, this cannot be confined to primary visual areas for its conceptual representation (Martin, 2016). In fact, some studies have demonstrated dissociation between the perception of color and the knowledge of color typicality associated with objects (Miceli et al., 2001; Samson & Pillon, 2003; Stasenko, Garcea, Dombovy, & Mahon, 2014). While such patient studies have generally supported grounded theories of semantics, we turn our attention towards the nature of the categories themselves in these studies- in particular, the

category of fruits/vegetables, which has proven relevant yet controversial. Samson and Pillon (2003) described patient (RS) who presented with a deficit in identifying the appropriate colors associated with fruits/vegetables, yet demonstrated intact color knowledge. Similarly, another patient (AC) displayed a comparable deficit, but was not disproportionate impaired in fruits/vegetables compared to other living categories as would be expected by a grounded theory (Miceli et al., 2001). This latter interpretation is drawn from evidence that has further fractionated both the natural category and its corresponding sensory properties. For instance, it has been proposed that animals and fruits/vegetables may differentially load on visual information, with the former relying more on form and the latter on color (Breedin, Saffran, & Coslett, 1994; Humphreys & Forde, 2001). Indeed, some studies have supported a facilitation of color in the classification and naming of fruits/vegetables (Rossion & Pourtois, 2004). However, in a study by Scorolli and Borghi (2015), it was shown that a distortion in shape rather than color was more detrimental to the correct identification of fruits/vegetables.

Artificial entities- namely manmade tools- on the other hand, have been shown to rely largely on functional information. The importance of action-related knowledge to the concept of tools has been argued on the basis of dorsal region activation (associated with the "where" pathway; Goodale & Milner, 1992) to the viewing (Chao & Martin, 2000; Mahon et al., 2007) as well as the naming of tool stimuli (Rumiati, Weiss, Shallice, Ottoboni, & Noth, 2004). Beauchamp and colleagues (2002) further demonstrated that motion particularly associated with tools and utensils is processed in a different region of the lateral temporal cortex than that related to human motion. Recently, it has also been

shown that decoding of activity related to viewing images of graspable objects could be achieved in somatosensory cortices (F. W. Smith & Goodale, 2015). However, neuropsychological evidence has not always converged with neuroimaging findings. For instance, some apraxic patients with damage to the left posterior parietal cortex have presented with an inability to execute proper tool use yet retain an ability to name tools (Negri et al., 2007). Apraxia, defined by the deficit for object use in the absence of a deficit in object identification, is typically associated with lesions to the left inferior parietal lobule (a "tool-naming" region; Mahon & Caramazza, 2009). Taken together, there is obviously ongoing debate as to the principles of neural organization and if the conceptual representation of a category is truly situated in perceptual and motoric subsystems (for a review supporting amodal theory, see Lambon Ralph, Jefferies, Patterson, & Rogers, 2017).

The current study aims to explore the extent to which the sensory property of color and the functional property of manipulability are integral to the representation of fruits/vegetables and tools, respectively. Framed differently, we wish to address if color and manipulability are processed as conceptual 'primitives'- that is, automatically accessed at the conceptual level of a given category (Martin, 2016). While a vast amount of the literature investigating the relationship between categories and properties has been concentrated on neuroimaging data, electrophysiological measures can perhaps provide a more fine-grained analysis of semantic meaning. A widely used index of semantic processing is the N400 component- a negative deflection in the waveform peaking at about 400ms post stimulus onset- that responds to the semantic 'predictability' of a stimulus in a given

context (for a review, see Kutas & Federmeier, 2011). This component has commonly been elicited by priming paradigms in which the association between a prior stimulus (prime) and target stimulus is measured: greater negativity indicates a reduction in relatedness of prime-target pairing (Kutas & Federmeier, 2011). Mcpherson and Holcomb (1999) used picture-picture priming of real objects belonging to various categories and found that unrelated target pictures led to greater negativity in the N400 time window. Similar effects have also been observed for cross-modal priming using both real objects (Kiefer, 2001) and line drawings (Nigam, Hoffman, & Simons, 1992) paired with words. In a study by Geukes and colleagues (2013), it was also shown that the degree of negativity of the N400 component could be modulated by the degree of prime-target relatedness. This finding is particularly pertinent to the current study, which aims to compare the effect of a prime subjected to visual feature modification on subsequent target processing.

Prior EEG research already speaks to its ability to distinguish between perceptual and semantic sources of activation (Kiefer, 2001). Moscoso del Prado Martin and colleagues (2006) investigated the spatio-temporal activity patterns of color-related versus form-related words, providing evidence for earlier peak processing of color compared to form and topographies that mapped to different underlying neural sources. Furthermore, Amsel and colleagues (2014) utilized a go/no-go semantic decision task to demonstrate that an incongruent attribute of a given object (e.g., purple – lime), when paired together, elicited an N200 component in response to the task demand of no-go. This N200 effect was also demonstrated in a similar task for incongruent action-related knowledge referring to

graspable objects (Amsel, Urbach, & Kutas, 2013). The authors interpreted these results in support of grounded views of cognition, maintaining that the neural circuitry responsible for perceiving and acting on objects, at least in part, play a role in their conceptual access from long-term memory (Barsalou, 2008).

In the current study, we presented participants with a lexical decision semantic priming paradigm previously demonstrating a double dissociation in reaction time performance between fruits/vegetables modified in color and utensils modified in orientation, results supporting modality-specific theory (for a more detailed account of design and theory, see *Chapter 1*). Using real objects as primes, we hoped to retain as much sensory information of the concept as possible while manipulating single dimensions. We simultaneously recorded EEG to investigate the effect of a perceptual modification of a real object prime on the conceptual processing of the target as indexed by the N400 component. Furthermore, given the multidimensional space of EEG data, exploratory analysis was performed using principle component analysis (PCA) and linear classification. Previous studies have successfully utilized PCA (Rastle, Lavric, Elchlepp, & Crepaldi, 2015) and semantic-decoding algorithms (Simanova, Gerven, Oostenveld, & Hagoort, 2010) to disentangle representations at the neural level. Ultimately though, the hypothesis is that a color-modified prime paired with a word representing a fruit or vegetables and an orientation-modified prime paired with a word representing a tool will be processed as a semantic violation and manifest as an N400 effect.

Methods

Participants. Forty native speakers of Italian partook in the experiment. Thirty-two participants remained post-processing of the data (for details, see *Analysis* section). Participants were healthy, right-handed (confirmed by the Edinburgh Handedness Inventory; Oldfield, 1971) individuals (mean age ± standard deviation = 24.33 ± 2.45; range = 19-30 years; 18 females/15 males) recruited via an advertisement posted on a dedicated social-networking site and monetarily compensated (25€) for their participation. All participants had normal or corrected-to-normal visual acuity, no history of neurological or psychiatric illness, and no history of drug or alcohol abuse that might compromise cognitive functioning. All participants were naive to the purpose of the experiment and provided informed written consent. The experiment was part of a program that was approved by the ethics committee of SISSA.

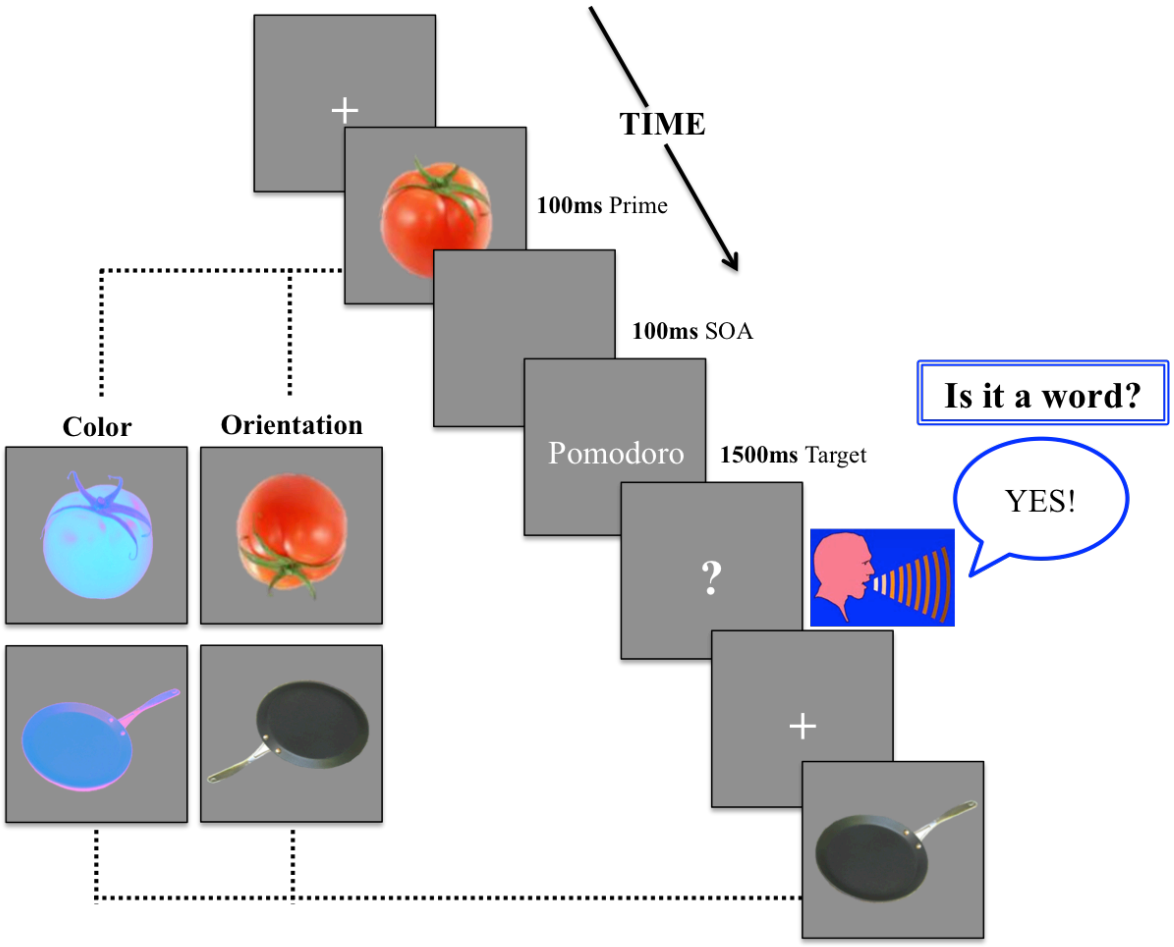
Materials. Forty-two Italian words served as critical target stimuli for the experiment. Twenty–one of these represented natural objects (fruits/vegetables; e.g., *pomodoro*, tomato) and twenty–one represented artificial objects (kitchen utensils; e.g., *forchetta,* fork). Each target word was associated with three different prime images, representing the corresponding object: (i) in its canonical color and position[2] (identity prime); (ii) with a clearly non–standard color (color modified prime); (iii) with a clearly non–standard position (orientation–modified prime). Identity primes were all taken from the FRIDa database (Foroni, Pergola, Argiris, & Rumiati, 2013). For a detailed description of prime

[2] In the case of objects without a clear canonical base position (e.g., knife; see Vannucci & Viggiano, 2000), the original image was chosen to be that with maximum affordability for a right–hand grasp (Tucker & Ellis, 1998).

image modifications and lexical properties of target words, refer to the *Materials* section of Chapter 1. For the purpose of the lexical decision task, 42 nonwords were created as further target stimuli. They were created from real words by either vowel inversion or single consonant substitution (e.g., *pentalo* from the Italian word *pentola*, pot). These targets were also associated with prime images, similarly to the word–target stimuli. To avoid repetition effects, three groups of participants were used, each being presented with a subset of the stimuli (only one condition of each prime object).

Procedure. Participants were seated approximately 60 cm from a 48 cm diagonal monitor (resolution: 1280 x 1024 pixels; aspect ration 4:3; refresh rate: 120Hz). Participants were presented with a lexical decision-priming paradigm similar to the one explained in Chapter 1 (for a schematic representation, see Figure 1).

Figure 1. *Schematic of trials of normal condition with color and orientation modification conditions shown to the left. A response to the question "Is it a word?" were vocalized on 25% of trials.*



On each trial, a prime image was followed by a target string (screen duration: 1500 ms) and participants were asked to silently judge if the string of letters presented was a word or nonword. However, on approximately 25% of trials, a question mark appeared following the target string, prompting a vocalized response. This was to ensure that participants were engaged in the task while minimizing any motor-related contamination introduced by a

button press (Vliet et al., 2014). Each target string was associated with one question mark to ensure that participants could correctly classify all target strings.

Overall, one block of the experiment consisted of 84 trials (42 words and 42 nonwords), which was repeated over five blocks. Stimuli were presented using E-Prime 2.0 Professional (Schneider, W., Eschman, A., and Zuccolotto, 2012). The experiment was performed in a sound-proof cabin. All electrical devices that were not sources of direct current and could interfere with EEG wave acquisition were turned off before experiment onset. During the experiment, ambient lighting was created using a LED lamp.

EEG Acquisition. Continuous EEG was recorded from an array of 128 silver-chloride biosemi active electrodes mounted on an elastic cap (topographic placement: radial ABC layout system). Two external electrodes were placed on the left and right mastoids (A1, A2) as reference. However, due to high impedance values for some participants, mastoids were later discarded and average reference used. EEG signal was amplified using a Biosemi Active-Two amplifier system (Biosemi, Amsterdam, Netherlands) at a sampling rate of 1024 Hz. Ground consisted of two separate electrodes: Common Mode Sense (CMS) active electrode with a Driven Right Leg (DRL) passive electrode. The direct current offset was kept below 25 mV. Data acquisition was made using the software Actiview605-Lores (www.biosemi.com).

EEG Preprocessing. EEGLAB (Delorme & Makeig, 2004) and Fieldtrip (http://www.ru.nl/neuroimaging/fieldtrip)- open source Matlab toolboxes- were used to

perform all preprocessing steps. Off-line data preprocessing included a digital high-pass filter of 0.1 Hz (as recommended by Tanner, Morgan-Short, & Luck, 2015) and a low-pass filter of 100 Hz. Data were downsampled to 256 Hz and segmented into epochs of 1400 ms, starting 200 ms before prime onset. Before proceeding with data cleaning, incorrect trials were identified and removed. Incorrect classification of a target string resulted in all trials in which that string appeared being removed. Electrodes exceeding a certain z-score threshold (kurtosis = 4; probability = 4; spectrum = 3) were removed from the data (Delorme, Sejnowski, & Makeig, 2007). A subset of electrodes sensitive to ocular movements were withheld from this threshold check and later passed to Independent Component Analysis (ICA). Noisy trials were deleted by visual inspection and data were referenced to the average. ICA using the Infomax algorithm was performed on all data for elimination of artifacts related to ocular and muscular movements. Data were time-locked to the onset of the prime image and baseline (200 ms pre-prime onset) removed. Automatic trial rejection was then performed for a more fine-grained cleaning: ±50 dB threshold in the 0-2 Hz frequency range (for capturing residual eye movements) and +25 to -100 dB in the 20-40 Hz (for capturing muscle movements). Finally, missing electrode data were interpolated to the original 128-electrode montage.

Data and ERP Analysis. Of the initial 40 participant sample, only 32 participants were retained for the analysis. One participant was eliminated due to high error rate (8.3% trials) and the remaining seven due to excessive noise (> 25% of trials were rejected). Error rate was less than 1% (M = 0.7; SD = 1.2) and the average number of trials rejected due to noise was less than 15% (M = 86.67%; SD = 6.6%) for the remaining subjects.

ERPs were computed for epochs extending from 200 ms pre-prime onset to 1000 ms post-target onset (1400ms duration). ERP analysis was performed using threshold-free cluster-enhancement (TFCE), which combines permutation-based statistics for significance testing (Mensen & Bern, 2014) over the entire epoch. While cluster-based statistics have been gaining momentum within the EEG community, cluster size/mass techniques require the arbitrary selection of the initial cluster-forming threshold value, which can have dramatic consequences on the overall expanse of each cluster in both time and space (Tillikainen, Salli, Korvenoja, & Aronen, 2006). The advantage of TFCE is that it uses information about both the intensity and the spatial distribution of the signal to enhance weak but broadly supported signals to the same numerical values as strong but highly focal signals. This is achieved through the implementation of two weighting parameters, without having to select a cluster-forming threshold a priori (for a more thorough description, see Mensen & Bern, 2014). Furthermore, TFCE has been shown to outperform other clustering methods in best controlling for type 1 error rate (Pernet, Latinus, Nichols, & Rousselet, 2015).

Principle Component Analysis (PCA). The hypothesis-driven approach to the data was complimented with a data-driven approach in order to explore any underlying effects between conditions not overtly present in the ERP analysis. Waveforms were subjected to PCA (Donchin & Heffley, 1978) in both the temporal and spatial domain. PCA is a suitable data-reduction approach for high-dimensional space that can be thought of as revealing internal structures in the data that a direct measurement of amplitude in a predefined set of electrodes or time points may not capture. Conversely, it may also

confirm trends that are observable in the ERP amplitudes. Data were first orthogonally transformed in the time domain with Varimax rotation, which resulted in a series of uncorrelated components ordered according to the amount of variance explained. The component extraction criterion was a cumulative variance explaining at least 70% of the data (Stevens, 1986). After time component selection, data were then retransformed into the original data space and subjected to spatial PCA, with an identical rotation and extraction criterion. The resulting component scores were then passed onto a linear regression analysis employing the mixed models approach. Further details are explained the *Results* section.

Classification Searchlight Analysis. Searchlight classification was performed on all electrodes in the interval of 250 to 500 ms post-target onset, corresponding to the typical N400 time window (Kutas & Federmeier, 2011). This was considered an exploratory analysis driven by the findings from the ERP and PCA analyses. Two types of analyses were performed: linear support vector machine (SVM) classification and linear discriminant analysis (LDA) classification. The SVM classifier is able to discriminate between two discrete classes of input whereas LDA uses an algorithm that is able to handle input of more than two classes; LDA utilizes a data reduction technique to divide the feature space based on maximum variance, similar to PCA, and generates weights to discriminate between classes (Subasi & Gursoy, 2010).

LDA classification was performed separately for the natural category (all conditions included) and then artificial category (all conditions included). SVM was performed on

two combinations of the dataset: the normal condition was combined with the color condition and then with the orientation condition, for the artificial category.

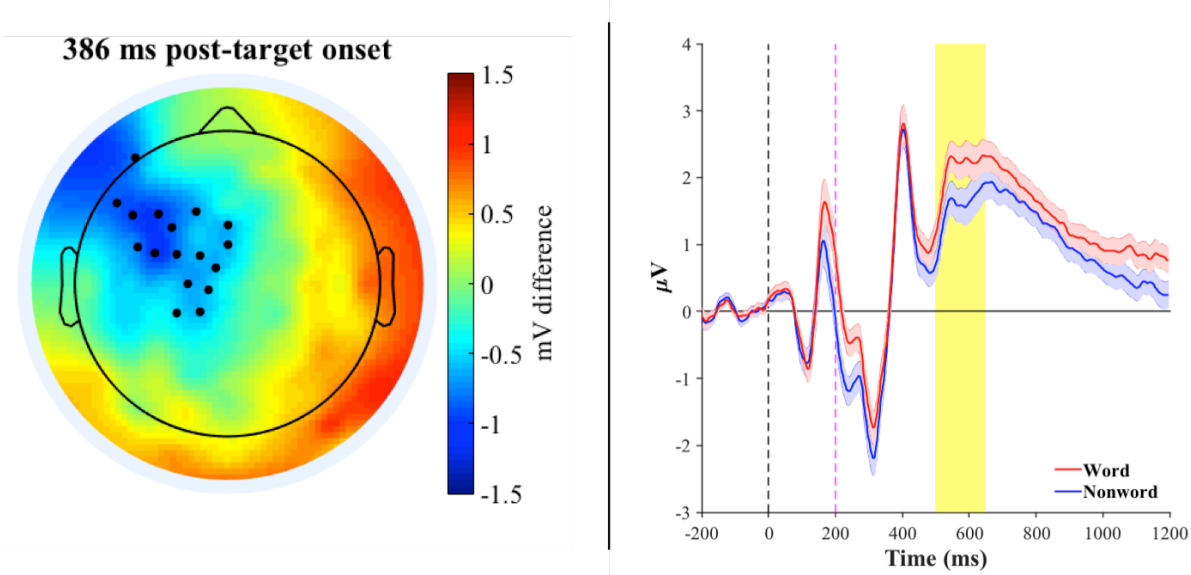
Classification was performed at the individual participant level. For each participant, all trials were submitted to the classifier. In cases where conditions contained different numbers of trials, a random subset of trials from the larger condition was sampled to match. Both classification algorithms employed a cross-validation measure and an odd-even partition scheme whereby both even and odd runs served as training and testing sets.

A searchlight approach was used to create neighborhoods of channels with each channel serving as 'origin' and identifying neighboring sensors within a certain configuration. Neighbors were defined based on a triangulation algorithm in Fieldtrip that allows for the building of triangles of 'nodes' that are independent of channel distances. Each neighborhood consisted of approximately 8 electrodes on average (M = 7.9; SD = 1.52; range = 6 - 12). Classification was then performed on each searchlight neighborhood across the entire scalp. Accuracies were generated per comparison, per participant, which were then thresholded for significance at the group-level using monte carlo permutation testing with 10000 iterations and corrected for multiple comparisons using TFCE. Such correction of the group-level stats involved a subtraction of the chance probability from all accuracies and randomly flipping the sign of the difference. This resulted in a z-score map that could be plotted for significance.

Results

ERP results. A first comparison of interest was between all word and nonword trials, irrespective of prime pairing. Average waveforms were calculated for each participant and a grand average made to compare conditions. Figure 2 shows the grand average of a cluster of channels whose activation significantly differed between word and nonword conditions along with a topographical map displaying the greater negativity for the nonword condition in the N400 time window. TFCE analysis showed that nonword trials had lower amplitudes than word trials for 19 unique channels in the left fronto-central region for the time range of 288 – 423 ms (peak channel at 389 ms: C1; $T = -6.27$; $p < 0.002$). This finding is in line with previous semantic literature that has demonstrated an N400 effect for meaningless compared to meaningful stimuli (Kutas & Federmeier, 2000). Nonword trials were discarded from further analysis and an emphasis placed on the experimental manipulation among word trials.

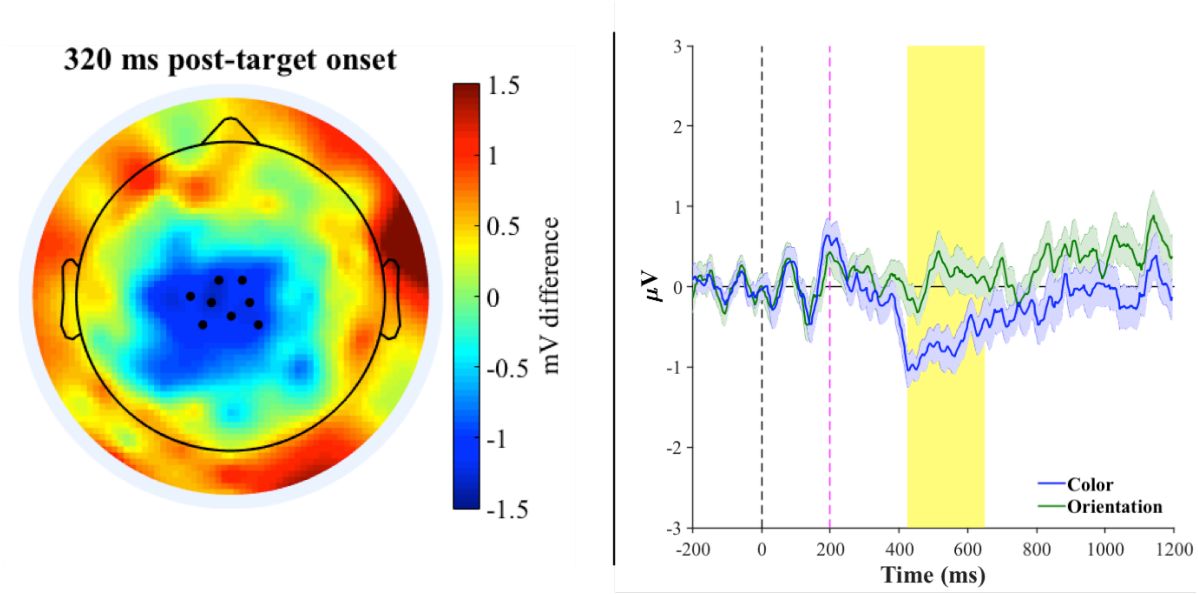
Figure 2. *Topographic map and mean waveforms for the comparison Word versus Nonword. Left panel- Topographic map of the brain at peak channel significance (~400 ms post-target onset). Topography reflects the difference in the grand average of Word – Nonword trials. Black dots represent significant electrodes at $p < 0.002$. Right panel- Mean waveform of the cluster of 19 unique channels significantly different at $p < 0.002$ in the time window 287 – 424 ms post-target onset. Dashed black line indicates the onset of the prime and dashed pink line the onset of the target. Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the N400 time window (300 – 450 ms post-target onset). Note: Negative is plotted downward, against convention.*



Word trials were divided by category into those representing natural versus artificial entities. For each category, difference waves were first generated for the color and orientation conditions by subtracting the normal condition, which served as baseline. Bonferroni correction was applied within each category, considering both planned and unplanned comparisons between each condition comparison (3 comparisons per category ~ $p < 0.017$) unless otherwise specified.

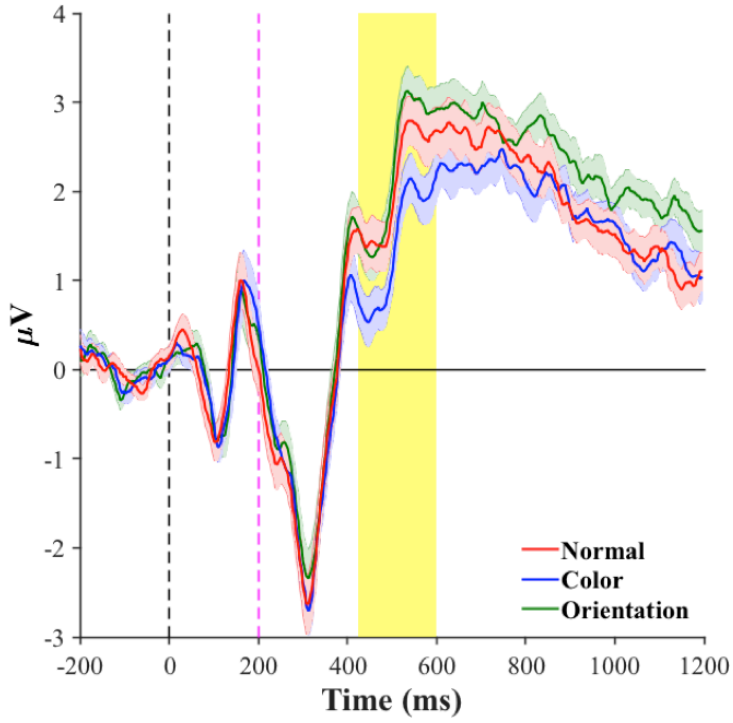
For the natural category, TFCE analysis showed that there was a significant difference between the [color – normal] and [orientation – normal] conditions, with color trials displaying lower amplitudes than orientation trials; this effect was found for 8 unique channels in the central region for the time range of 299 – 381 ms (peak channel at 323 ms: B1; $T = -6.07$; $p < 0.001$). For a plot of the results and brain topography, see *Figure 3*.

Figure 3. *Topographic map and mean waveforms for the Natural category. Left panel- Topographic map of the brain at peak channel significance (~320 ms post-target onset). Topography reflects the difference of the difference waves of Color – Orientation trials (after Normal baseline was subtracted). Black dots represent significant electrodes at p < 0.001, bonferroni corrected. Right panel- Mean waveform of the cluster of 8 unique channels significantly different in the time window of 299 – 381 ms post-target onset. Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the N400 time window (225 – 450 ms post-target onset). Note: Negative is plotted downward, against convention.*



However, as can be noted from the figure, [orientation – normal] resulted in a positive waveform in the time window of interest, indicating that the orientation condition did not elicit an N400 response in relation to baseline; rather there was greater positivity. Average waveforms for the significant channels from the comparison [color – normal] and [orientation – normal] were then taken for each condition separately and the resulting plot displayed in Figure 4.

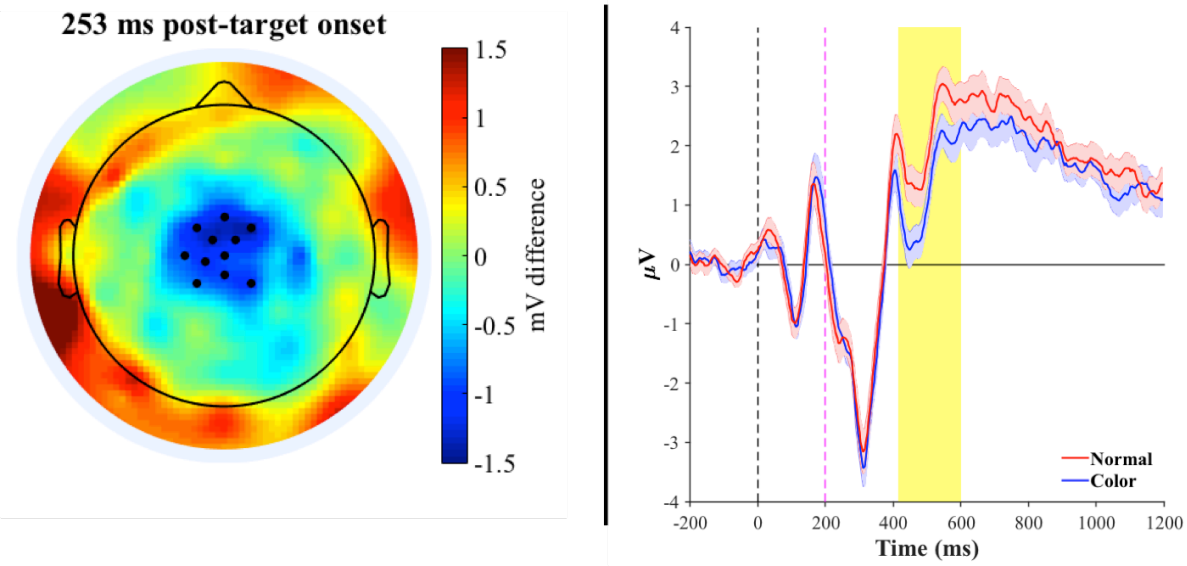
Figure 4. *Mean waveform of the cluster of 8 unique channels identified from the comparison of the difference waves in Figure 3 (Natural category). Regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the N400 time window (225 – 450 ms post-target onset). A visualization of the waveform demonstrates that the orientation condition elicited a greater positivity in the N400 time window with respect to the normal condition (nonsignificant), whereas the color condition elicited the canonical N400 (significant; comparison explored in Figure 5). Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the N400 time window (225 – 450 ms post-target onset). Note: Negative is plotted downward, against convention.*



Although ultimately a direct comparison between the orientation and color conditions yielded a significant effect, the question remained as to whether or not a feature change in prime would exert a semantic violation effect in the N400 time window as compared to the normal priming condition. Therefore, color and orientation conditions were directly compared to the normal baseline.

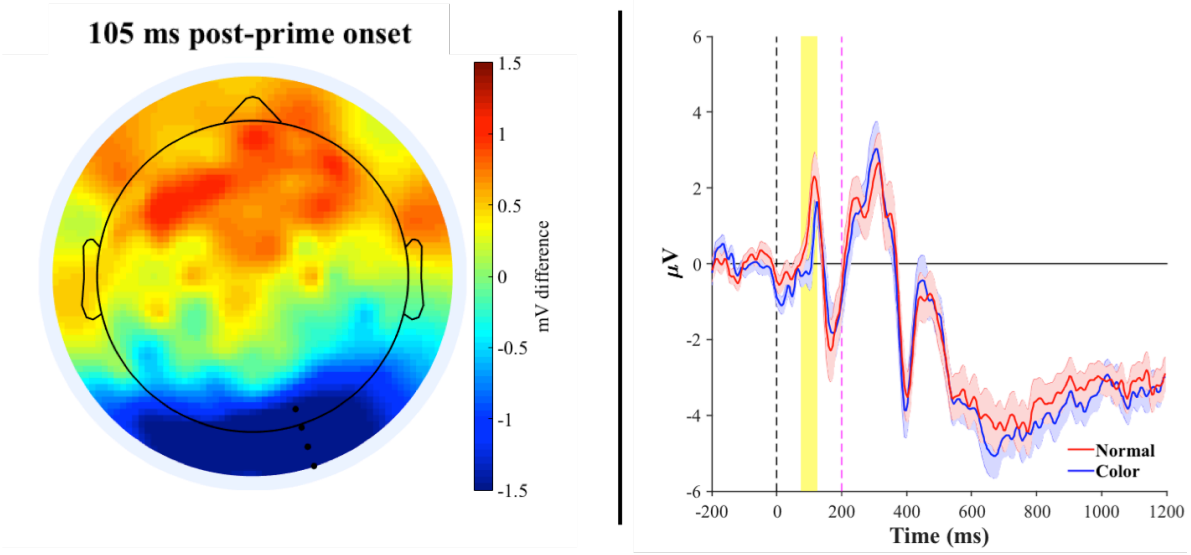
TFCE analysis showed that color trials had lower amplitudes than normal trials for 11 unique channels in the left fronto-central region for the time range of 213 – 387 ms (peak channel at 256 ms: C1; $T = 6.12$; $p < 0.009$). The resulting brain topography and waveforms can be seen in Figure 5. This is line with the hypothesis that a color-modification for fruits/vegetables would yield a semantic violation as indexed by an increase in N400 amplitude. For the orientation condition, only one channel exhibited higher amplitude compared to the normal condition, in the centro-parietal region for the time range 89 – 97 ms (peak channel at 93 ms: Pz; $T = -5.88$; $p < 0.05$, uncorrected).

Figure 5. *Topographic map and mean waveforms for the Natural category. Left panel- Topographic map of the brain at peak channel significance (~253 ms post-target onset). Topography reflects the difference of Color – Normal waveforms. Black dots represent significant electrodes at p < 0.009, bonferroni corrected. Right panel- Mean waveform of the cluster of 11 unique channels significantly different in the time window of 213 – 387 ms post-target onset. Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the N400 time window (213 – 400 ms post-target onset). Note: Negative is plotted downward, against convention.*



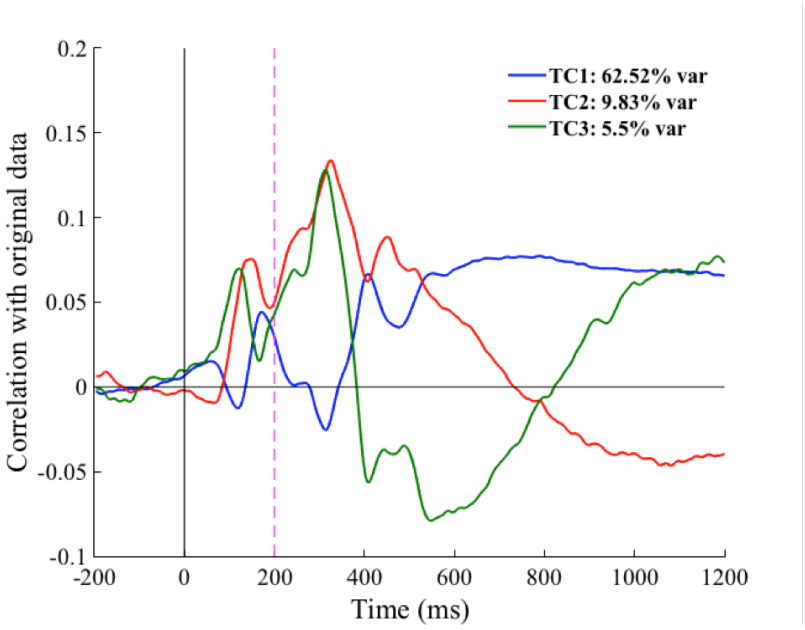
Next, experimentally manipulated conditions were individually compared to the normal condition for the artificial category. TFCE showed a significant cluster of 4 unique channels displaying lower amplitude for color compared to normal condition, resembling a reduction in the P1 component for color-modified images (peak channel at 102 ms (post-prime): A26; $T = -6.6$; $p < 0.05$, uncorrected; see Figure 6 for the brain topography and waveform plot). This is unsurprising given that the P1 can reflect attentional modulation of a given stimulus (Luck, Woodman, & Vogel, 2000). Comparing between the orientation and normal condition, there were no significant channels at any time point ($p > .1$).

Figure 6. *Topographic map and mean waveforms for the Artificial category. Left panel- Topographic map of the brain at peak channel significance (~105 ms post-prime onset). Topography reflects the difference of Color – Normal waveforms. Black dot represents the significant electrode at $p < 0.05$, uncorrected. Right panel- One unique channel was significantly different in the time window of 89 – 97 ms post-target onset. Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the time window (50 – 150 ms post-target onset). Note: Negative is plotted downward, against convention.*



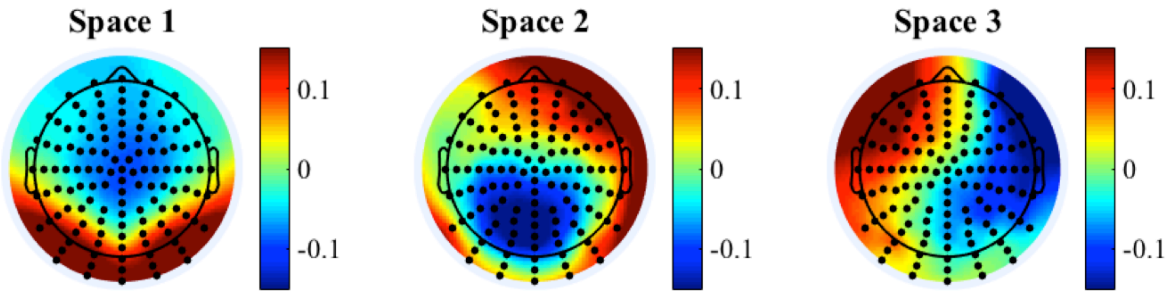
PCA results. A data matrix of amplitudes with 358 time points as variables and 24576 cases (128 channels * 32 participants * 3 conditions * 2 categories) were subjected to temporal PCA and three components extracted with cumulative variance explaining ~77.85% of the data. For a plot of the loadings, which represent the contributions (correlation) of the original data to the formation of each respective component, see Figure 7. Time component 1 accounted for the highest amount of variance in the data (62.5%,), which likely reflects general task-induced properties of the signal that is shared variance among all trials. Time component 2, on the other hand, accounted for 9.8% of the total variance and seemed to largely comprise a response to both prime and target stimulus. Time component 3, accounting for 5.5% of all variance, was of greatest interest, however, as its formation reflected contributions of data coming from the N400 time window.

Figure 7. *Plot demonstrates the correlation of the original data with the first three time components extracted from PCA. Notice that the third time component, explaining 5.5% of the variance, had a shape resembling the broad peaking observed in the N400 time window.*



Data in reduced temporal space were then subjected to spatial PCA with a data matrix containing 128 channels as variables and 576 cases (3 time components * 32 participants * 3 conditions * 2 categories). Three space components were extracted from the data, representing a cumulative variance explaining 73.6% of the data (see Figure 8 for topographical formation of each spatial component). As there were fewer assumptions made about the particular topographical configuration with which an effect would present, the focus is turned to the analysis of the component scores.

Figure 8. *Topographies of the correlation of the original data with the first three space components extracted from PCA.*



A total of 1728 component scores (3 time components * 3 space components * 32 participants * 2 categories * 3 conditions) were submitted to linear regression analysis using mixed effects modeling. Component score data were divided into temporal and spatial components and a mixed effects model created for each comparison with *condition* and *category* as fixed factors and *subject* as a random factor. The use of subject as a

random factor was the result of hierarchical model creation and testing using the AIC criterion, as explained in Chapter 1. Notably, there was a significant interaction between category and prime for time component 3-spatial component 1 (T3-S1) [$F(2, 155) = 3.09$, $p = .048$, $\omega^2 = .78$]. The model (M1) for time component 3-spatial component 1 with subject added as a random factor outperformed the simpler fixed effects model (M0), yielding a lower AIC value [M0 (AIC) = 2090; M1 (AIC) = 1936; $\chi^2(1)= 155.5$, $p < .001$]. In order to resolve the interaction effect and elucidate differences in condition between categories, data for T3-S1 were further divided into two separate models for natural and artificial trials.

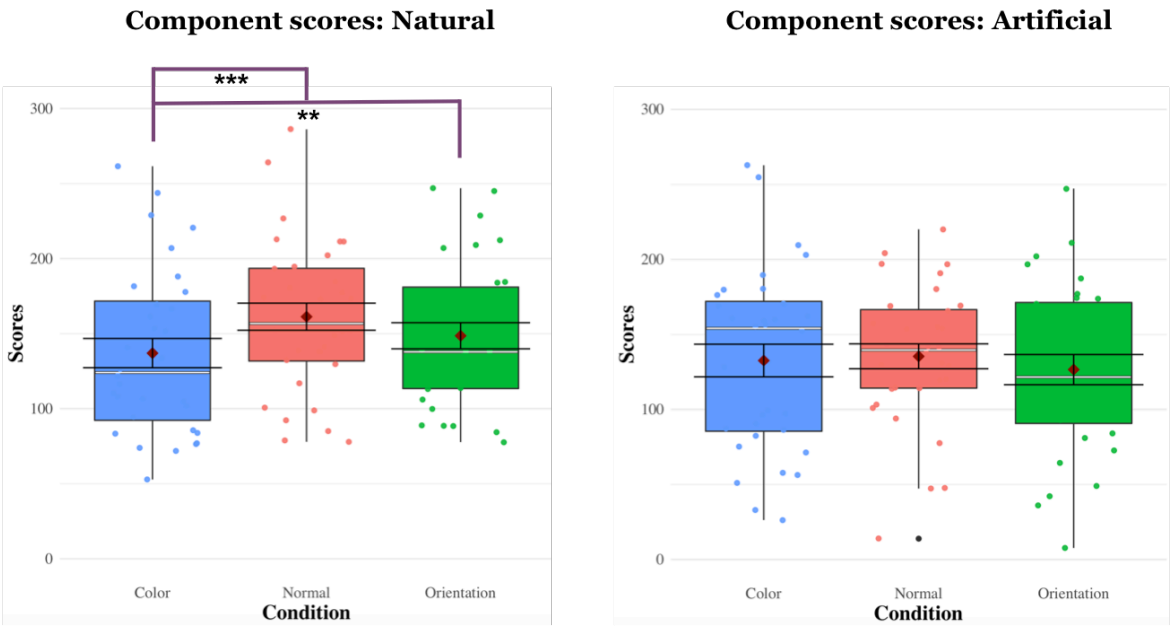
For the natural category, the main effect of condition [$F(2, 62) = 6.37$, $p = .003$, $\omega^2 = .8$] indicated that there was a significant difference between the normal and color condition ($t(62) = -3.382$, $p = .001$) and between the color and orientation condition ($t(62) = -2.68$, $p = .01$); see Table 1 for descriptive statistics).

Table 1. *Mean and SD of scores for Time Component 3- Space Component 1*

Condition	**Natural**		**Artificial**	
	Mean	SD	Mean	SD
Normal	161.29	9.03	135.41	8.33
Color	137.01	9.77	132.62	10.92
Orientation	153.4	9.68	126.54	10.1

However, there was no difference between the normal and orientation condition (p = .26) nor were there significant differences between conditions for the artificial category (interaction: p = .45). For a plot of the results from model T3-S1, see Figure 9.

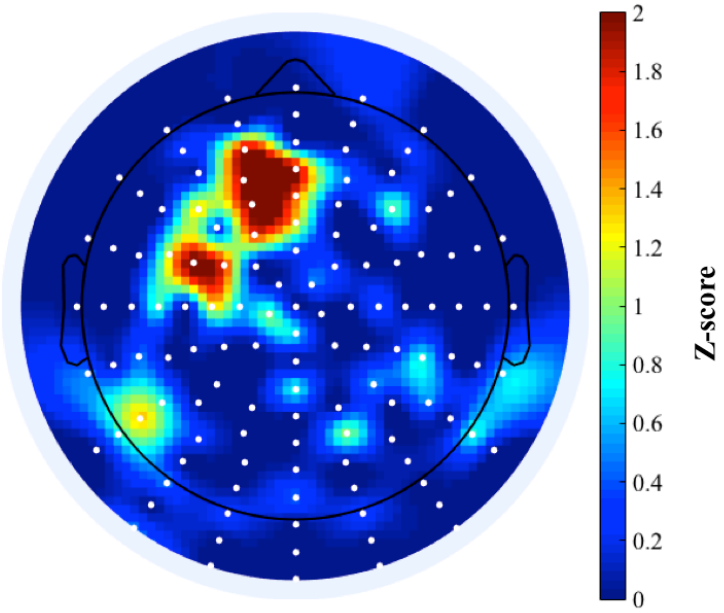
Figure 9. *A boxplot of component scores for the third time component – first spatial component, for both the Natural and Artificial category. The white line indicates the median for each condition, the red dot indicates the mean, and the two bars on either side of the red dot indicate the standard error of the mean. Each condition's scatterplot are of the individual scores per participant for a visualization of data spread. Asterisks denote significance at ** = 0.01 and *** = 0.001.*



Classification results. A statistical z-score map of LDA accuracies can be found in Figure 10. Significance was defined as a one-tail probability value of $z > 1.64$ ($p < 0.05$). For the natural category, the LDA classifier successfully discriminated between the three conditions in 7 channels as origin in the searchlight (z-range: 1.7 – 2.18; p-range: .015 -

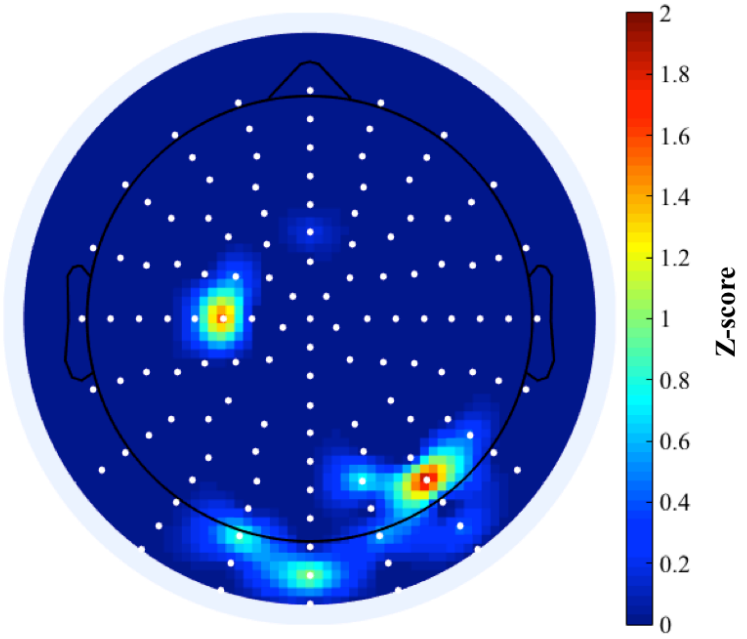
.045). These channels were located in the left fronto-central region and resembled the ERP scalp topography of significant channels for the word-nonword comparison as well as the natural category comparison, albeit to a lesser extent. These results confirm the robustness of the main finding that an exposure to a prime manipulation in a feature relevant to the categorization of the natural category of fruits/vegetables yields a semantic violation in the N400 time window.

Figure 10. *A statistical z-score map of LDA accuracies for the natural category. Significance was defined as a one-tail probability value of z > 1.64 (p < 0.05) and can be observed in 7 channels that served as searchlight origins (dark red regions) in left fronto-central sites.*



Interestingly, the SVM classifier could also distinguish between the normal and color (z = 2.11, p = .017) and the normal and orientation (z = 1.83, p = .034) conditions, but at one channel neighborhood site, both in the mid-frontal region (see Figure 11).

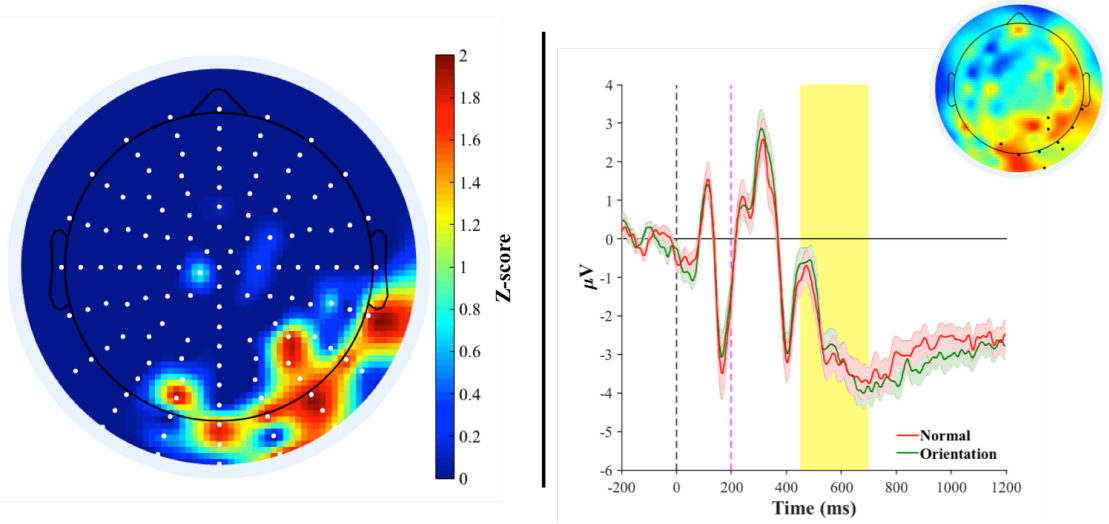
Figure 11. A statistical z-score map of LDA accuracies for the artificial condition. Significance was defined as a one-tail probability value of $z > 1.64$ ($p < 0.05$) and can be observed in 1 channel that served as searchlight origins (dark red regions) at a right posterior channel site.



For the artificial category, although there was no significant difference between conditions when comparing ERP amplitudes, one channel neighborhood was able to significantly discriminate between classes ($z = 1.9$, $p = .029$). Moreover, while the SVM classifier was unable to significantly distinguish between the normal and color condition, 10 channel neighborhoods were able to classify between the normal and orientation condition (z-range: 1.69 – 1.93; p-range: .027 - .046). This cluster of channels was located at right posterior scalp sites (see Figure 12).

The fact an effect did not emerge in the ERP amplitudes could attest to the loss of information when trials are averaged across conditions. This finding suggests that information in the prime window exerted a differential effect on the N400 time window, such that meaningful information distinguishing between conditions was contained at these channel sites.

Figure 12. . *Left panel- A statistical z-score map of SVM accuracies for the comparison between the normal and orientation conditions of the artificial condition. Significance was defined as a one-tail probability value of z > 1.64 (p < 0.05) and can be observed in 10 channels that served as searchlight origins (dark red regions) at right posterior channel sites. Right panel- Waveform of 10 channels at the right posterior scalp site with corresponding scalp topography at 351 ms post-target onset. Shaded regions along the waveforms indicate standard error of the mean. The shaded yellow bar denotes the time window (250 – 500 ms post-target onset). Note: Negative is plotted downward, against convention.*



Discussion

We presented people with a lexical identity priming paradigm as a means of assessing if modal properties of fruits/vegetables and tools were integrated with object knowledge at the conceptual level. We used real objects as primes and word/nonword targets to directly

access the concept associated with the prime at the basic level. The assumption was that if a feature is particularly relevant for a given category, then a distortion in that feature should result in a semantic violation as indexed by the N400 component.

Preliminary analysis first sought to confirm that the N400 was elicited for nonword compared to word trials. ERP analysis revealed this effect over left-lateralized fronto-central electrode sites. Although the maximal distribution has been reported over centro-parietal electrode sites, this distribution has been prone to fluctuation based on the eliciting stimulus; concrete words, for instance have demonstrated enhanced frontal activity (Kounios & Holcomb, 1994; Kutas & Federmeier, 2011).

For the natural category of fruits/vegetables, ERP component analysis demonstrated a significant effect in the N400 time window (i.e., 250 – 500 ms post-target onset) that was modulated by the manipulation in prime. A comparison of the difference wave [orientation – normal vs. color – normal] revealed a significant negative deflection for the color-modified condition. Interestingly, upon further inspection, it was observed that the magnitude of this difference was driven by a positive deflection of the orientation-modified condition with respect to the normal condition. This increased positivity for the orientation condition was a rather unexpected finding. Given the graded nature of the priming effect observed in the behavioral data of the previous chapter combined with an assumption of a 'graded' feature salience, it was hypothesized that an orientation-modification may also elicit an N400 effect, albeit to a significantly lesser extent than color. One plausible explanation for greater positivity could be that the perceptual relation

between the features could have yielded a differential response for the orientation condition. In a study by Pecher and colleagues (1998), in failing to observe perceptual priming in a lexical decision task, the authors reasoned that the priming effect is dependent on the overlap of the activated features and not the necessarily the defining features. The fact that the orientation-modified condition still contained the correct color property could have 'pre-activated' the concept and led to a reduction in the N400 component. Indeed, it has been argued that sensitivity to feature overlap can render an increase in positivity of N400 amplitudes (Federmeier & Kutas, 2001). However, as the resulting waveform did display such a deviance from the normal condition, the effect, in part, must have been modulated by the orientation change itself. One likely explanation is that functional knowledge is also relevant to the concept of fruits/vegetables, but has a neural signature that cannot be captured by the N400 component alone (e.g., propagation from an earlier component). Mcpherson and Holcomb (1999) manipulated the degree of prime-target relatedness and found that earlier epochs could distinguish between highly unrelated pairings whereas later epochs captured the more subtle intermediary degree of relatedness, arguing for two separable components- an N300 and N400- with differing scalp topographies.

In an attempt to optimally disentangle the ERP waveforms and expose any hidden trends in the data, we performed both temporal and spatial PCA. By dividing between components and conducting linear mixed model testing, we found a significant interaction between category and condition in the first spatial component of the third time component. Notably, the third time component exhibited a correlation (i.e., loadings, or eigenvectors)

with the original data that resembled an N400-like waveform pattern. This effect was driven by a significant difference between the normal and color condition of the natural category, although a graded contribution of the three conditions to the composition of this component was evident. If we reversely map these findings back onto the original data, we can infer as follows: the color condition of the natural category, displaying the lowest component scores, contributed the least to the formation of the third time component/first space component, consequentially, in the negative direction of correlation with the original data. Given their negative correlations with the original data at central electrode sites in the N400 time window, the two correlations can be multiplied to roughly reconstruct the direction of amplitude (positive) at that time in space. The graded component scores by condition reflect the graded contribution to the absolute positivity, the color condition contributing the least and the normal condition the most. This did not correspond exactly to the original ERP waveforms averaged from the significant channels; however, this is to be expected as first, PCA provides projections of the data in unitless dimensional space and second, reflects the entire topography, rendering a direct overlap with specific channels impossible to discern. Furthermore, the fact that the reduced color component scores aligned with a reduction in amplitude positivity for the color condition could attest to the stability of the N400 component for the color relative to the normal condition and a possible broader distribution over scalp sites.

LDA and linear SVM classification were also performed. Similar to PCA, LDA is another technique for creating linear combinations of the data based on maximum variance but generates a hyperplane based on weights to distinguish between multiple classes (Subasi &

Gursoy, 2010) whereas SVM tries to optimize separability between two classes of data by maximizing the margin, or distance (Bhuvaneswari & Satheesh Kumar, 2013). Significant LDA classification accuracy was observed at fronto-central channel sites with a slightly left-lateralized bias; this pattern of results resembled the ERP scalp topography of significant channels for the word-nonword comparison as well as that of the color vs. normal condition comparison, albeit to a lesser extent. SVM classification could also accurately distinguish between the color vs. normal and orientation vs. normal conditions, although only at one channel neighborhood site. LDA and SVM employ different algorithms in the classification process. LDA's superior ability to discriminate between conditions could be due to the fact that it projects the data into a space that is based on feature extraction of dimensions common to all input, to avoid redundancy, and maximizes the difference between classes.

Ultimately, our ERP findings and more advanced data-mining techniques converged to indicate a direct involvement of perceptual color processing on conceptual access to fruits/vegetables, providing support for grounded, modal views of semantic cognition. Moreover, PCA demonstrated a graded tendency of contribution across the three conditions to the construction of a time and space component central to the N400 effect. Classification analysis further confirmed discriminability between the three conditions, indicating that an orientation modification also elicits an effect on conceptual processing of fruits/vegetables. These findings align well with the behavioral data from the previous chapter, which showed a reduced priming effect for orientation-modified fruits/vegetables. Why should fruits/vegetables, as instances of the natural kind, be sensitive to an

orientation change? Fruits/vegetables have generally proven to be an elusive category in the semantic literature; patient studies of differing profiles have provided inconsistent patterns of deficit. In some cases, patients with difficulty in identifying fruits/vegetables have been spared in naming animals (Hillis & Caramazza, 1991) while others have demonstrated the inverse pattern (A. Caramazza & Shelton, 1998). This has led to the proposition that it be labeled as a dissociable category from the living/nonliving distinction. An alternative hypothesis could be that it demonstrates properties that are relevant to both. A recent study by Netelenbos and Gonzalez (2015) investigated automatically-evoked motor affordances in images of graspable objects including fruits/vegetables and found a facilitation of categorization when asked to overtly respond to the graspability of the object. This facilitation was only observed, however, when the task required the engagement of action knowledge, suggesting that conscious processing may be necessary. Here we show evidence for what we interpret to be automatic activation of action affordance at the conceptual level, as would be expected by an orientation manipulation (Tucker & Ellis, 1998).

Conversely, ERP component analysis of the artificial category did not reveal a significant difference in the time window of interest. The only significant finding was a slight shift and reduction in the P100 (P1) component to the color compared to normal condition. This could easily be due to low-level perceptual differences in the prime image; the P1 component has shown to be sensitive to external properties of the stimulus like luminance, which can consequently exert an influence on attention (Luck et al., 2000).While brightness was matched between conditions, it was difficult to control for all subject

measures of color sensation; thus, the perceptual salience of a blue-hued object could have generated a pop-out effect. The fact that there was no observable N400 could suggest that action knowledge relating to manipulability is not automatically engaged at the conceptual level. However, other factors might have contributed to the absence of this effect. For instance, higher values of Coltheart's N, which is a measure of orthographic neighborhood size (Coltheart, Davelaar, Jonasson, & Besner, 1977), has been shown to elicit N400s of smaller amplitude (Holcomb, Grainger, & O'Rourke, 2002). The artificial category did possess higher values of Coltheart's N with respect to the natural category, which could have mitigated an effect. And although the PCA analysis also did not show a significant difference between conditions, the orientation condition displayed a lower mean component score compared to the normal condition.

On the other hand, both LDA and SVM classifiers were able to significantly discriminate between conditions in the N400 time window. For SVM classification, 10 channel neighborhoods at right posterior scalp sites were able to distinguish between the normal and orientation condition. Interestingly, a recent study by Hauser and colleages (2015) combined fMRI with EEG to show the scalp topography related to the hand motor area as defined by ROI analysis and found a similar pattern of activity at right-lateralized posterior sites. Although a plot of the average waveform (see Figure 12) at significant channel sites reveals a plateauing of the peak in the orientation condition around ~300 ms post-target onset and an extended negativity at later time points, no obvious difference between conditions can be interpreted prima facie. Some studies have supported a later processing stage for action knowledge compared to sensory knowledge (Amsel, Urbach, & Kutas,

2013; Moscoso del Prado Martin, Hauk, & Pulvermueller, 2006), which could suggest a later time course for semantic integration for tools. In fact, the results from the quartile distributions of RT performance from Chapter 1 would also corroborate a slight shift in the window of processing of tools; however, when we trained and tested the classifier at later time points, it performed at chance. The fact an effect did not emerge in the ERP amplitudes could most likely attest to the loss of information when trials are averaged across conditions and finer-grained analysis necessary (Murphy, Poesio, Bovolo, Bruzzone, & Dalponte, 2011) and could suggest greater inter-subject variability of neural response. This finding suggests that information in the prime window exerted a differential effect on the N400 time window, such that meaningful information distinguishing between conditions was contained at these channel sites despite the absence of an effect at the level of grand mean.

In the current study, we employed a lexical identity priming paradigm to automatically tap into conceptual representations of fruits/vegetables and tools. We provide strong evidence that color is an integral sensory property to the conceptual representation of fruits/vegetables. To a lesser extent, action knowledge relating to manipulability is also automatically engaged at the conceptual level, but this effect is not directly relatable to N400 component and only significantly emerged at one channel neighborhood site in the classification analysis. Conversely, although tools did not demonstrate a significant difference in waveform between conditions in the ERP analysis, the SVM classifier could distinguish between the normal and orientation conditions at 10 channel sites, indicating that orientation did exert a differential effect on the semantic processing of tools. Taken

together, the results support modal theories, whereby modality-relevant input is integrated at the conceptual level.

CHAPTER 3

Introduction

Neuroimaging studies have identified regions within the ventral temporal cortex that preferentially respond to different categories of object representations. For instance, in a seminal work by Kanwisher and colleagues (1997), a specialization for faces was found in a portion of the right fusiform gyrus (i.e., fusiform face area- FFA). Theoretical motivation for such a discovery came from patients with damage to the right occipitotemporal region of the cortex who jointly demonstrated a selective deficit for recognizing faces (De Renzi, 1997). Additionally, viewing buildings and scenes has consistently activated a posterior region of the parahippocampal cortex known as the parahippocampal place area (PPA; Epstein & Kanwisher, 1998), with further evidence provided by patients that demonstrated a deficit in visuospatial processing related to landmark identification (Ploner et al., 2000). The link between patient profiles from the neuropsychological literature and functional specialization for certain categories is a strong one. Disproportionate deficits in the ability to name living entities (e.g., animals, fruits/vegetables) compared with nonliving entities (e.g., tools) have raised important questions as to the structure of conceptual knowledge (for a review, see Capitani, Laiacona, Mahon, & Caramazza, 2003).

According to some accounts, a medial-to-lateral gradient in bilateral regions of the fusiform gyrus is responsible for the processing of tools versus animals, respectively, on the basis of peak activations (Chao et al., 1999). Furthermore, animals have been shown to activate the superior temporal sulcus, which is a region associated with biological motion (Bonda, Petrides, Ostry, & Evans, 1996), whereas activation in the left posterior medial

temporal lobe has been observed for motion-processing particularly related to tools (Martin & Chao, 2001). Proponents of the sensory/functional theory have interpreted these findings as support for distributed subsets of modality-specific regions that are differentially engaged based on the type of category (Martin, 2007). It has, however, been argued that some patients who have presented with a deficit for living entities have demonstrated equal impairment for both sensory and functional properties (Caramazza & Shelton, 1998). In light of these findings, alternative theory was put forth highlighting the evolutionary significance of a privileged few categories that are processed in anatomically distinct neural regions (Caramazza & Shelton, 1998). Known as the Domain-Specific Knowledge Hypothesis (DSKH), such a model claims that animals, tools and plant life are processed as discrete "neural" categories and that this processing is constrained by connectivity between higher- and lower-order brain regions (for an in-depth discussion, see Mahon & Caramazza, 2011). Despite diverging theory as to the distribution of processing across categories, all accounts have come to agree on the essentiality of connectivity to this processing.

Several studies have investigated the relationship between functional specialization for specific categories and their connectivity to other regions in the brain. Within the parahippocampal cortex, PPA has shown to be more functionally connected with unimodal areas such as V4, reinforcing its importance in the processing of visuospatial information (Aminoff, Kveraga, & Bar, 2014). Others have employed resting-state connectivity to identify a core network for face processing that includes FFA, the inferior occipital gyrus, and superior temporal sulcus (Zhang, Tian, Liu, Li, & Lee, 2009). A typically left-

lateralized network of regions associated with different aspects of tool processing has also been identified (i.e., Tool Processing Network; Garcea & Mahon, 2014). Viewing manipulable artifacts has led to differential activity in regions such as the posterior middle temporal gyrus (associated with the mechanical motion of tools; Beauchamp, Lee, Haxby, & Martin, 2002), the inferior parietal lobule (associated with object manipulability and motor imagery; Lewis, 2006), and other regions that diverge along ventral-dorsal pathways depending on the type of information invoked. Thus, a distribution of processing regions is responsible for the integration of information in the representation of tools.

An important but arguably underinvestigated category in the semantic literature is that of fruits and vegetables. Neuropsychological patient studies have shown it to be a category that dissociates from the canonical living/nonliving distinction (Blundo et al., 2006; A. Caramazza & Shelton, 1998; Hart et al., 1985; Hillis & Caramazza, 1991), with a pattern of deficit that can potentially be mapped to both natural and artificial domains. A cross-theoretical perspective would suggest specialized regions for the processing of fruits and vegetables, although no network has been formalized, to date. From an evoluationary perspective, DSKH postulates the importance of plant life among the evolutionary relevant categories within the conceptual system. From the perspective of feature-based accounts, the importance of color (Bramão, Faísca, Forkstam, Reis, & Magnus, 2010), form (Haxby et al., 2001), and motion (Beauchamp et al., 2002) to the processing of concepts would hypothesize a distributed network associated with categorically-relevant information, especially given that fruits and vegetables possess a high within-category structural similarity that would necessitate a greater reliance on features, such as color, to resolve

competition (Humphreys, Price, & Riddoch, 1999). Furthermore, in terms of a medial-to-lateral gradient of processing, some researchers have argued for a gradient based on an inanimate/animate distinction as opposed to a nonliving/living one (Connolly et al., 2012). Given that fruits and vegetables do not possess biological motion yet are considered living entities, it would be interesting to see where they may fall along this gradient.

In the current study, we used a localizer task to identify regions associated with the processing of images of fruits and vegetables. Participants were presented with grayscale images of fruits and vegetables, animals, tools, faces, and insects in a block-design fashion of passive viewing. Insects were included as a separate category due to the fact that little is known about their neural signature, though some research has placed it on the inanimate end of an animate-inanimate continuum (Connolly et al., 2012). However, an analysis of insects was outside the scope of the present chapter and will be reported at a future time. We hypothesized that the conceptual processing of fruits and vegetables will yield activation in regions responsible for unimodal processing of visual properties such as color (for a case study of color impairment, see Stasenko, Garcea, Dombovy, & Mahon, 2014) in addition to down-stream processing regions that may preferentially 'connect' with category-specific regions in the ventral temporal cortex. Such privileged connectivity has been proposed as a constraining factor to the partial activational overlap observed in the ventral cortical processing stream (Stevens et al., 2015) and would allow for the flexible access to the multiple nuances of category-relevant information. We adopted a multi-dimensional approach to identifying a network involved in the processing of fruits and vegetables through localization, connectivity analysis, and multivoxel pattern analysis to

elucidate the underlying neural correlate.

Methods

Participants. Participants were 16 healthy, right-handed native speakers of Portuguese (mean age ± standard deviation = 20.44 ± 3.24; range = 18-28 years; 13 females/3 males) recruited as a convenience sample, mainly from an introductory level psychology course, those of who received course credit. All participants had normal or corrected-to-normal visual acuity, no history of neurological or psychiatric illness, and no history of drug or alcohol abuse that might compromise cognitive functioning. All participants provided written informed consent.

Stimuli. Stimuli were images of objects belonging to one of five categories: animals, fruits/vegetables (FV), faces, tools, and insects. Twelve items were used for each category, with four exemplars for each item, yielding a total of 240 images. The original high-resolution images were collected from the World Wide Web as open source or taken from internal image databases or the FRIDa database (Foroni, Pergola, Argiris, & Rumiati, 2013). Images were converted to grayscale, downsized to a resolution of 400 x 400 pixels, and presented on a gray background. Stimuli were matched for brightness between categories [F (4, 235) = .415, p = .8]. However, due to intrinsic differences in object categories, it was not possible to match for size and spatial frequency, which were determined according to the same method employed in Chapter 1 (ratio of white/black pixels from object masks for size and fast fourier transform for spatial frequency). However, t-test showed that, for spatial frequency, there was no difference between FV

and Animals ($p = 0.95$) or Tools ($p = .22$) and between Tools and Animals ($p = .12$). For the category of Faces, however, there was a difference between all category comparisons ($p < 0.001$). For a list of items presented, see Table 1.

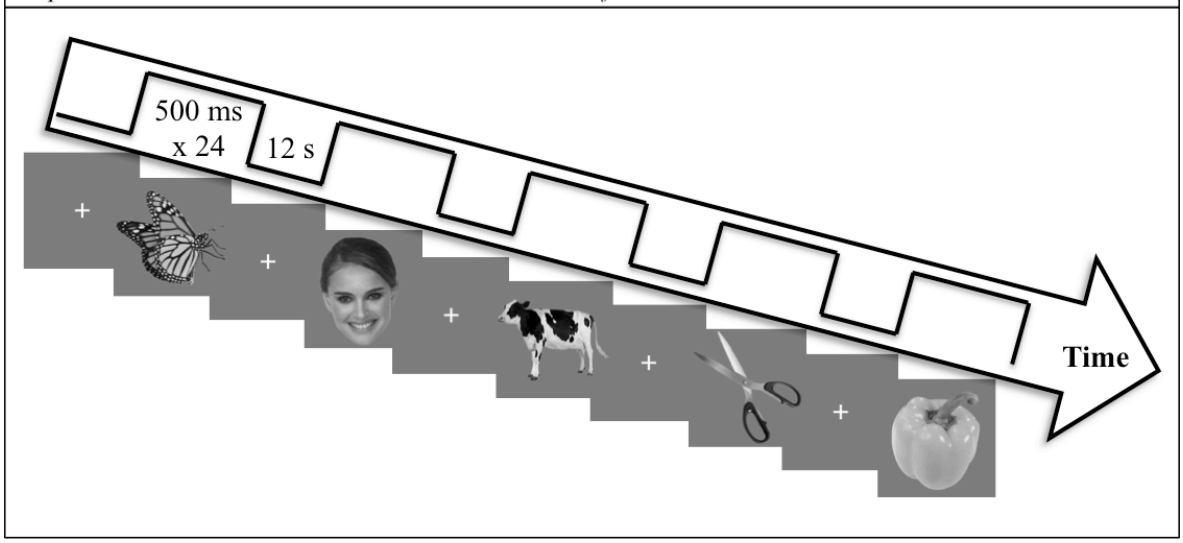
Table 1. *List of stimuli used in the experiment.*

Category				
Animals	*Faces*	*Fruits/Vegetables*	*Insects*	*Tools*
Bear	Halle Berry	Apple	Ant	Corkscrew
Cat	Sandra Bullock	Banana	Bee	Fork
Cow	Angelina Jolie	Broccoli	Beetle	Hammer
Deer	Natalie Portman	Cabbage	Butterfly	Knife
Dog	Julia Roberts	Cherry	Caterpillar	Pan
Elephant	Kate Winslet	Eggplant	Dragonfly	Pliers
Giraffe	Alec Baldwin	Mushroom	Firefly	Razor
Horse	Tony Blair	Pepper	Fly	Saw
Lion	George Bush	Pineapple	Grasshopper	Scissors
Monkey	Tom Cruise	Pomegranate	Ladybug	Screwdriver
Pig	Matt Damon	Strawberry	Moth	Shovel
Rabbit	Robert De Niro	Tomato	Wood Louse	Teapot

Procedure. During the fMRI scanning session, participants were presented with a standard multicategory block-design task. Participants were asked to passively view the screen as images were presented in rapid succession (for a schematic representation, see Figure 1). Stimulus presentation was controlled using Psychtoolbox in MATLAB (Brainard, 1997). Stimuli were back-projected on an LCD monitor positioned ~65 centimeters from the end of the scanner bore. Participants viewed the screen through a tilted mirror that was

mounted on the head coil. Images subtended a visual angle of approximately 10°. The design consisted of 10 runs with each run comprising 10 blocks or the equivalent of two miniblocks for each of the five categories. Each block consisted of 24 images that were presented sequentially for 500 milliseconds each (total of 12 s). Blocks were interleaved with periods of fixation that were equal in duration (12 seconds). Blocks were then pseudo-randomized within each run such that no more than 2 blocks of the same category occurred consecutively. Each run lasted approximately 4 minutes 32 seconds.

Figure 1. *fMRI paradigm- Participants were presented with blocks of images, each belonging to one of five categories. Per block, each image lasted 500 milliseconds, with 24 images presented in succession. Experimental blocks were interleaved with a 12 second fixation block.*



MRI Acquisition. MRI data were collected using a Siemens Magnetom Tim Trio 3T MRI scanner with a 32-channel head coil at the Portuguese Brain Imaging Network (Institute of Nuclear Sciences Applied to Health; ICNAS) of the University of Coimbra. For each subject, a high-resolution T1-weighted anatomical image was acquired using a magnetization prepared rapid gradient-echo pulse sequence (repetition time (TR) = 1900

ms; echo time (TE) = 2.32 ms; flip angle = 9°; slice thickness = 0.9 mm; field of view (FOV) = 256 mm; acquisition matrix = 256 x 256; voxel size = 0.9 x 0.9 x 0.9 mm; single-shot ascending slice sequence). For the task-based functional localizer, an echo-planar imaging (EPI) pulse sequence was used for the T2* contrast (repetition time (TR) = 2000 ms; echo time (TE) = 22 ms; flip angle = 90°; slice thickness = 2.3 mm; field of view (FOV) = 220 mm; acquisition matrix = 256 x 256; voxel size = 2.3 x 2.3 x 2.3 mm; 40 descending interleaved even-odd slices). The first two volumes of each run were discarded from further data processing to allow for magnetic saturation effects. Foam padding was used to reduce head movement within the coil.

MRI Data Preprocessing. MRI data were preprocessed using BrainVoyager software package version 2.8 (Goebel, Esposito, & Formisano, 2006) and customized in-house scripts implementing the BVQX toolbox for MATLAB. For each subject, anatomical images were interpolated to a 1 x 1 x 1 mm voxel size, deskulled, and transformed into standardized Talairach space (Talairach & Tournoux, 1988). Functional images underwent a series of preprocessing steps in the following order: slice time correction (sinc interpolation), motion correction aligned to the first volume of the first functional run, and linear detrending in the temporal domain (2 cycles within run cutoff). Each subject's functional data were then coregistered to their own T1 anatomical image. For the univariate analysis, functional data were smoothed with a 6 mm fullwidth half maximum (FWHM) Gaussian kernel whereas for the multivariate analysis, data were lightly smoothed with a 2.5 mm FWHM (Op de Beeck, 2010) and then interpolated to a 2 x 2 x 2

mm voxel size. Due to excessive head motion (> 2.3 mm = one voxel), between one and three runs were eliminated from 6 of the participants.

fMRI GLM Analysis. Conditions of interest from the functional localizer data were convolved with a standard two-gamma hemodynamic response function. The general linear model (GLM) was used to fit beta estimates to the conditions of interest. Six head motion parameter estimates were also included as nuisance variables to attract variance attributable to head motion. Group-level analysis treated participants as a random factor; thus, there were 15 degrees of freedom in the group-level analysis. Data underwent z-transformation in order to normalize the influence of inter-subject variability. The five regressors of interest were the five categories of stimuli: animals, FV, faces, tools, and insects. A contrast analysis was performed between select categories with a focus being placed on [FV > all other categories]. However, the contrast between FV and insects was not considered due to the category of insects being a poorly understood and underrepresented category in the literature without substantial evidence for its neural signature.

Psychophysiological Interaction (PPI). ROIs exhibiting a preference for FV were used as seed regions in the PPI analysis. These regions were identified based on the contrast [FV > Animals, Tools, and Faces] and included the left and right fusiform, the left and right lingual gyrus, and a portion of the inferior parietal lobule (angular gyrus- PGp).
In order to elucidate which regions in the brain may be connected to the seed regions of interest, whole-brain PPI analysis was performed on the raw time series data. PPI is a type

of effective connectivity that investigates the task-dependent changes in coupling between two regions; the purpose is to determine which voxels in the brain increase their relationship with a given seed region as a function of the task (Friston, 2011; Reilly, Woolrich, Behrens, Smith, & Johansen-berg, 2012). For the current experiment, generalized PPI was utilized as more than two categories were presented. It has been shown that the generalized form of context-dependent PPI potentially reduces both false negatives and false positives (Mclaren, Ries, Xu, & Johnson, 2012), the high proportion of false negatives being a problematic element in this type of analysis (Reilly et al., 2012). The resulting GLM included five PPI terms (one for each category), the five psychological time courses, and the physiological time course of the seed region (the latter two being considered covariates of no interest). Five GLMs in total were created, one for each of the seed ROIs.

MVPA Classification Searchlight. Multivariate pattern analysis (MVPA), which tests the discriminability of neural patterns among categorical comparisons of interest, was implemented in MATLAB using custom scripts and the framework provided by CoSMoMVPA toolbox (Oosterhof, Connolly, Haxby, & Rosa, 2016). Searchlight classification of all category pairings was attempted using linear support vector machines (SVM). This resulted in six classification procedures for each combination of interest (FV vs. Tools, FV vs. Animals, FV vs. Faces, Tools vs. Animals, Tools vs. Faces, and Animals vs. Faces). All combinations were considered rather than only those that concerned FV due to the fact that either category in the pairing could be driving a significant classification

result. In this way, all classification output could be superimposed and regions corresponding to the processing of FV identified.

A spherical searchlight (Kriegeskorte, Goebel, & Bandettini, 2006) comprising a subset of the voxels was used and classification was performed throughout the whole brain with each voxel serving as center of the searchlight. For adequate sensitivity, a 35-voxel sphere (~4mm) was chosen to avoid the pitfall of too few voxels being uninformative or too many voxels reducing specificity (Etzel, Zacks, & Braver, 2013).

Classification was performed at the individual participant level. GLMs were created separately for each individual participant based on the volume time courses that were lightly smoothed with a 2.5 mm FWHM smoothing kernel. β-weights were calculated for each mini-block of each run, which resulted in 20 β-weights per voxel on which classification was performed. Classification training and testing were done using an n-fold cross-validation strategy. Classification performance was recorded as the proportion of correct guesses from all iterations of the cross-validation procedure and was allocated to the central voxel of each searchlight, generating a map of accuracies. Accuracy maps were then combined across all participants and group-level significance testing performed using monte carlo simulations with 10,000 iterations and corrected for multiple comparisons using TFCE (Smith & Nichols, 2009). This produced a z-score map that could be p-thresholded and visualized for areas of significant accuracy.

Representational Similarity Analysis (RSA) Searchlight. An important method of identifying areas in the brain that may selectively respond to a particular experimental condition is by comparing the activation patterns across voxels; when activation is associated with a given condition, the corresponding activity patterns can be considered as a representation of it (Kriegeskorte, Mur, & Bandettini, 2008). If we not consider conditions as classes of stimuli, both within-class and between-class comparisons can be made by calculating pairwise correlations in activity patterns for each stimulus presentation. By comparing these patterns associated with each pair of stimuli, one can obtain a dissimilarity matrix that characterizes the representation. This representational dissimilarity matrix (RDM) is composed of one value per comparison that is typically the correlational distance between conditions (1 – correlation), which normalizes for both mean and variability of activity (Haxby et al., 2001). Therefore, the RDM will be symmetric with the diagonal comprising zeros (no dissimilarity). For the purposes of the current experiment, pairwise comparisons were made between the β-weights across all stimuli presentations using a searchlight method. Each row of the matrix corresponded to β-weights for one miniblock of one category. As there were 20 miniblocks associated with each of the five categories, the resulting RDM consisted of 100 rows and columns. Hence, a dissimilarity value could be computed within each category (via pairwise comparisons of the 20 β-weights) as well as between categories.

Simple categorical models of category-preferring dissimilarities were created in order to identify voxels in which the RDM of the activity patterns were correlated with the model. For each category-preferring RDM, zero was given to all rows and columns representing

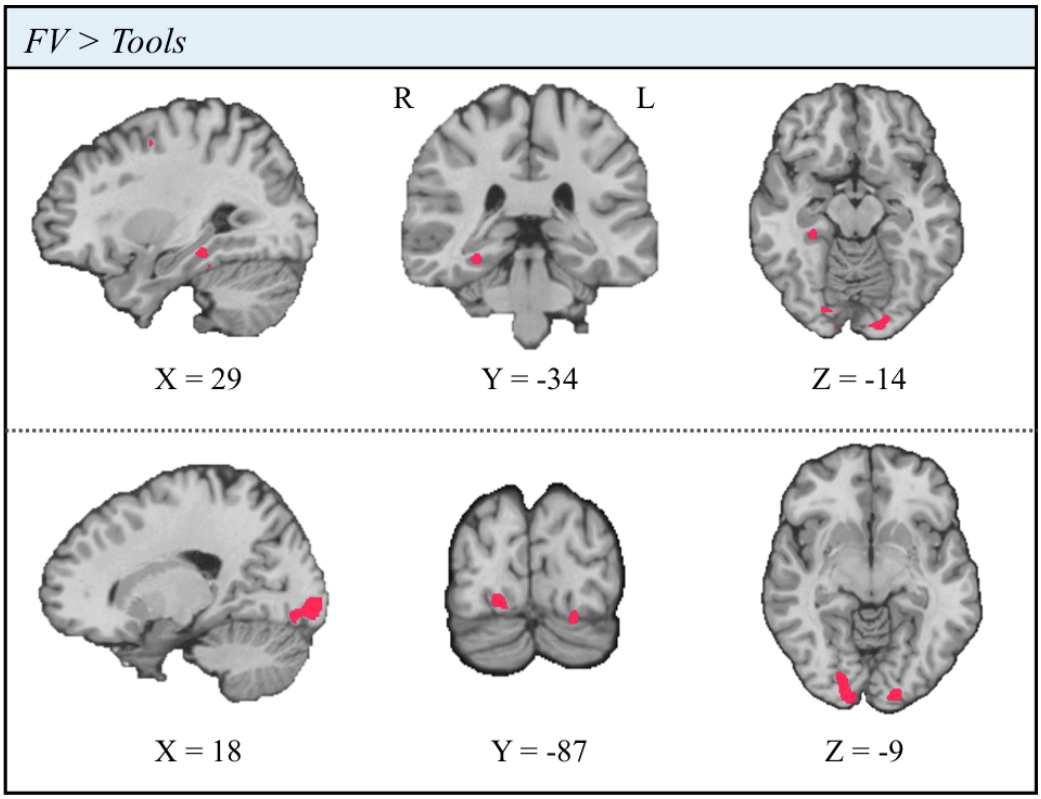
that category (perfect dissimilarity = 0) and 1 was given to all other categories. Thus, four different models were created and compared (FV, tools, animals, and faces). Having an RDM for the neural representation and an RDM for the theoretical model, the second-order dissimilarity (the dissimilarity of dissimilarity matrices) between the two was computed as a correlation coefficient. The correlation coefficient used was Spearman rank as a linear match should not be assumed (Kriegeskorte, Mur, Ruff, et al., 2008). Second-order RDMs were created for each searchlight, resulting in a Fisher-transformed z-score map per participant and monte carlo permutation statistics were used for inference at the group-level. The final output was a combined group-level statistical map for each category, which were then superimposed and compared.

Results

All reported group whole-brain contrast maps were FDR-thresholded at $p < 0.05$ unless otherwise specified. In a first analysis, individual contrasts between FV and all other categories (apart from insects) were considered in order to identify FV-preferring regions. The contrast [FV > all] was then performed in order to select prominent clusters that would be used in connectivity analyses. Finally, the contrast of each category against all others was considered to provide a more comprehensive understanding of the respective regions involved in their processing, with particular emphasis placed on the fusiform gyrus.

FV > Tools. As can be seen in Figure 2, the largest clusters were found in the right parahippocampal gyrus (peak voxel: 29, -34, -14), the right lingual gyrus (peak voxel: 14, -99, --4), and the left lingual gyrus (peak voxel: -17, -98, -6).

Figure 2. *Regions showing preference for FV > Tools. The regions identified include the left and right lingual gyri and the right parahippocampus. Note- Image presentation is left-right inverted.*



Prior research has shown that the parahippocampal cortex is connected to unimodal cortical regions, such as V4 (Aminoff et al., 2014), which aligns well with these findings. An exhaustive list of the activated regions and their corresponding peak voxels with significance values can be found in Table 2.

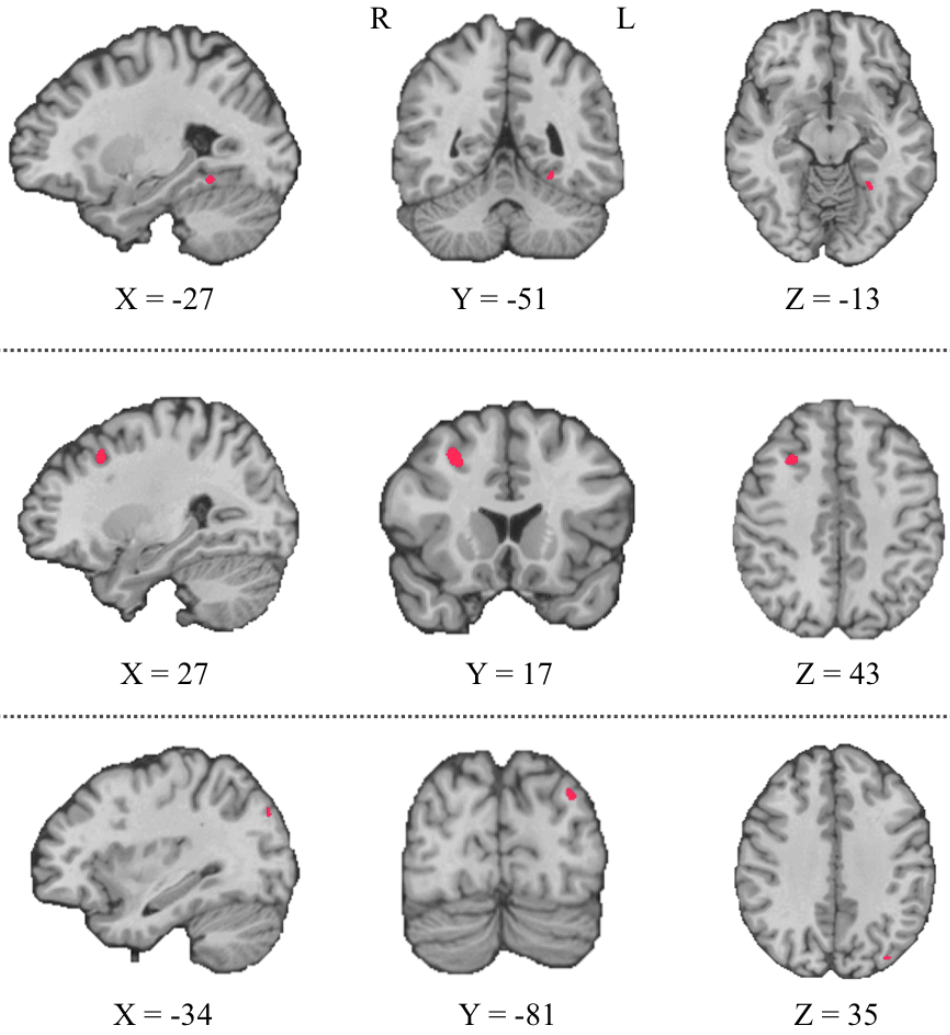
Table 2.
Talairach coordinates for peak voxels from regions showing differential BOLD contrast for ***FV > Tools***

Region	Hemisphere	Peak voxel coordinates (XYZ)			Statistical value for peak voxel	Volume (mm^3)
Parahippocampal Gyrus	Right	29	-34	-14	$t_{(15)}$=6.07, p < .001	127
Parahippocampal Gyrus	Right	29	-38	-22	$t_{(15)}$=4.49, p < .001	3
Inferior Parietal Lobule (angular gyrus)	Right	41	-79	27	$t_{(15)}$=4.49, p < .001	10
Middle Frontal Gyrus (posterior)	Right	28	-4	51	$t_{(15)}$=4.7, p < .001	19
Middle Frontal Gyrus (anterior)	Right	21	23	41	$t_{(15)}$=4.61, p < .001	9
Lingual Gyrus	Right	14	-99	-4	$t_{(15)}$=7.27, p < .001	1850
Lingual Gyrus	Left	-17	-98	-6	$t_{(15)}$=7.25, p < .001	1349

FV > Animals. As presented in Figure 3, clusters were located in the anterior portion of the right middle frontal gyrus (peak voxel: 27, 17, 40), the left medial fusiform gyrus (peak voxel: -27, -51, -13), the left inferior parietal lobule (caudal area of angular gyrus; Caspers, Eickhoff, & Geyer, 2008) (peak voxel: -36, -82, 35), and the superior parietal lobule (peak voxel: -49, -31, 37). Notably, these regions have previously been implicated in the tool processing network (Garcea & Mahon, 2014).

Figure 3. *Regions showing preference for FV > Animals. The regions identified include the right middle frontal gyrus and left-laterialized portions of the medial fusiform gyrus, the inferior parietal lobule, and the superior parietal lobule. Note- Image presentation is left-right inverted.*

FV > Animals



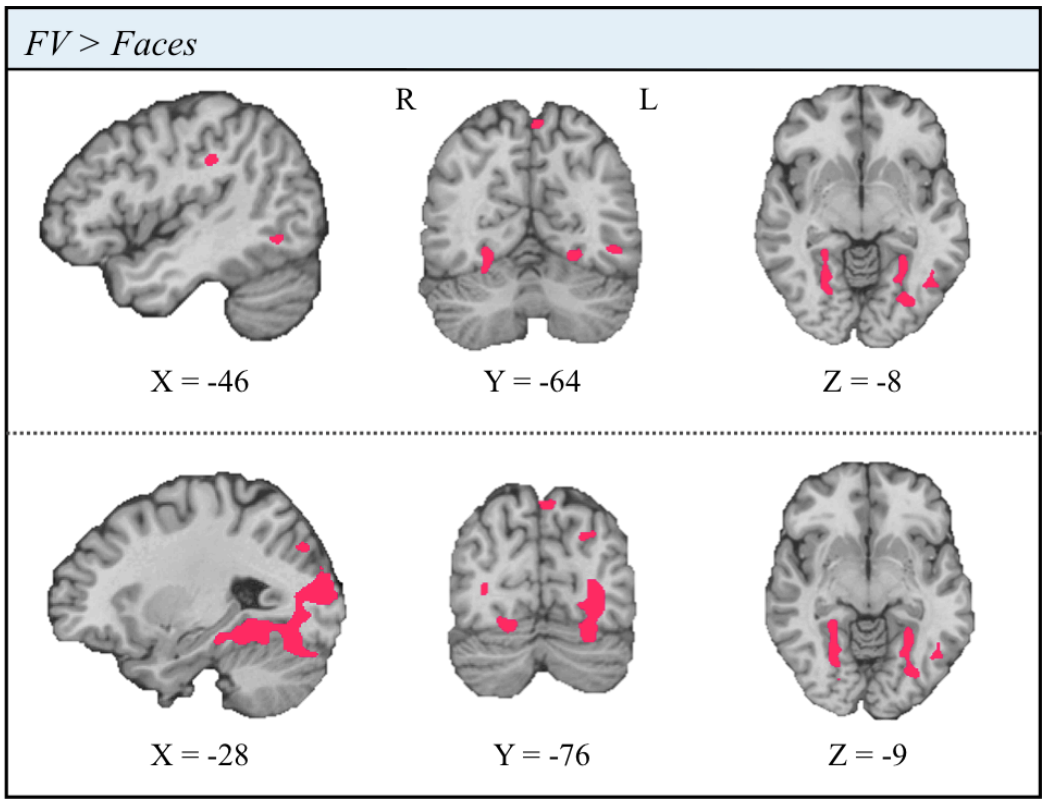
Activated regions and their corresponding peak voxels with significance values can be found in Table 3.

Table 3.
Talairach coordinates for peak voxels from regions showing differential BOLD contrast for ***FV > Animals***

Region	Hemisphere	Peak voxel coordinates (XYZ)			Statistical value for peak voxel	Volume (mm^3)
Middle Frontal Gyrus (anterior)	Right	27	17	40	$t_{(15)}$=6.65, $p < .001$	246
Fusiform Gyrus (medial)	Left	-27	-51	-13	$t_{(15)}$=5.17, $p < .001$	84
Inferior Parietal Lobule (angular gyrus)	Left	-36	-82	35	$t_{(15)}$=4.63, $p < .001$	44
Superior Parietal Lobe	Left	-49	-31	37	$t_{(15)}$=4.79, $p < .001$	19

FV > Faces. Broad areas of the bilateral fusiform gyrus were active as can be seen in Figure 4. Other areas of large cluster size included an area spanning both the posterior and anterior superior parietal lobe (peak voxel: -2, -74, 56), the left inferior parietal lobule (rostral area of supramarginal gyrus; (Zhang & Li, 2014) (peak voxel: -48, -29, 31), the right middle occipital/lingual gyrus (peak voxel: 19, -91, 3), the left lingual gyrus/visual association area (peak voxel: -33, -76, -7), and the left posterior middle temporal gyrus (peak voxel: -46, -63, -8).

Figure 4. *Regions showing preference for FV > Faces. The regions identified include broad areas of the bilateral occipital cortex, the left inferior parietal lobule, posterior and anterior portions of the superior parietal lobule, and the left posterior middle temporal gyrus. Note- Image presentation is left-right inverted.*



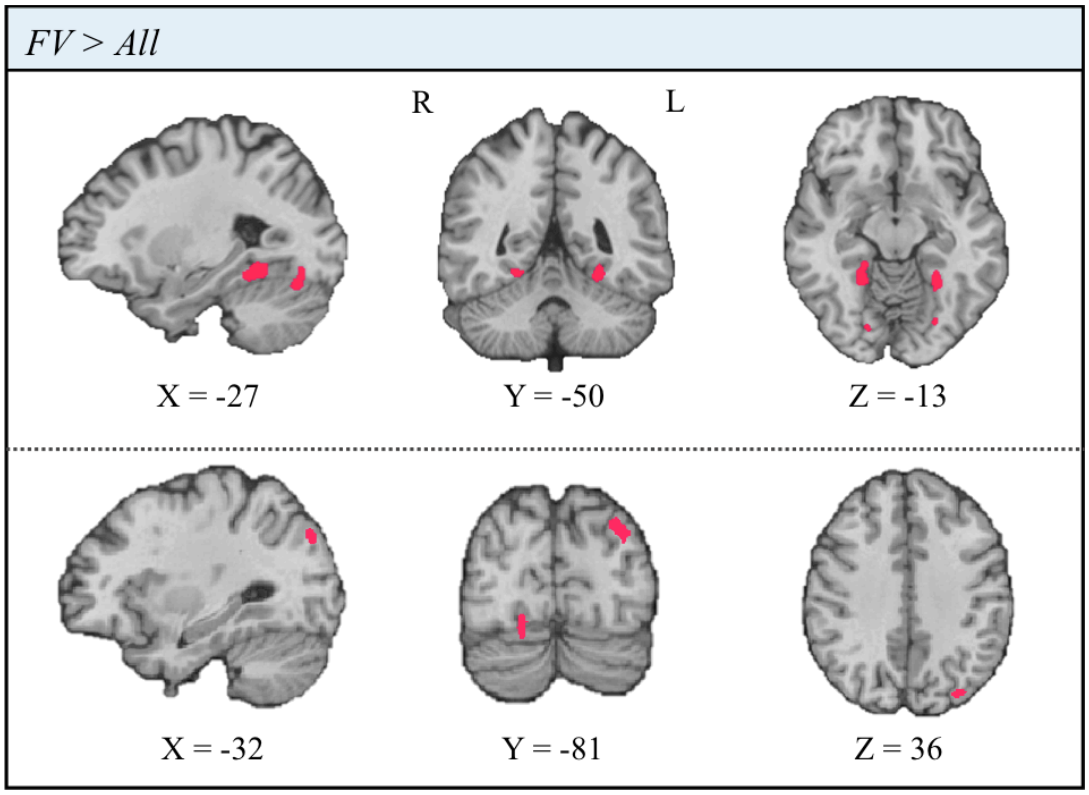
Although large areas of activation were found in visual processing regions of the cortex, areas typically associated with motor information were also activated. An exhaustive list of the activated regions and their corresponding peak voxels with significance values can be found in Table 4.

Table 4.
*Talairach coordinates for peak voxels from regions showing differential BOLD contrast for **FV > Faces***

Region	Hemisphere	Peak voxel coordinates (XYZ)			Statistical value for peak voxel	Volume (mm^3)
Cuneus/Middle Occipital Gyrus/Lingual Gyrus	Right	19	-91	3	$t_{(15)}$=7.99, p < .001	5643
Fusiform Gyrus (medial)	Right	24	-63	-12	$t_{(15)}$=6.58, p < .001	3438
Superior Frontal Gyrus	Right	28	25	46	$t_{(15)}$=4.39, p < .001	49
Caudate	Right	16	6	20	$t_{(15)}$=4.46, p < .001	14
Superior Parietal Lobe (posterior)	Right	6	-84	48	$t_{(15)}$=4.61, p < .001	585
Inferior Occipital Sulcus	Right	9	-97	-1	$t_{(15)}$=4.18, p < .001	32
Posterior Cingulate	Right	3	-43	5	$t_{(15)}$=4.82, p < .001	71
Posterior Middle Cingulate	Right	2	-24	38	$t_{(15)}$=4.37, p < .001	42
Superior Parietal Lobe (ant/post)	Left	-2	-74	56	$t_{(15)}$=6.26, p < .001	3418
Cingulate Gyrus (posterior)	Left	-2	-38	25	$t_{(15)}$=4.33, p < .001	42
Anterior Cingulate Gyrus	Left	-3	26	35	$t_{(15)}$=4.25, p < .001	18
Lingual Gyrus/ Cuneus/visual association area	Left	-33	-76	-7	$t_{(15)}$=7.21, p < .001	9916
Superior Parietal Lobule (anterior)	Left	-21	-68	56	$t_{(15)}$=4.1, p < .001	22
Inferior Parietal Lobule (supramarginal gyrus)	Left	-48	-29	31	$t_{(15)}$=5.55, p < .001	307
Middle Temporal Gyrus (posterior)	Left	-46	-63	-8	$t_{(15)}$=4.55, p < .001	242

FV > All. For this contrast, a 20-voxel threshold was set as a selection criterion for those clusters to be considered in the connectivity analyses. As can be seen in Figure 5, the largest clusters that emerged were in the left fusiform gyrus (peak voxel: -27, -50, -14), the right fusiform gyrus (peak voxel: 22, -51, -13), the left lingual gyrus (peak voxel: -27, -73, -21), the right lingual gyrus (peak voxel: 18, -81, -14), and the inferior parietal lobule (posterior angular gyrus; peak voxel: -35, -82, 36).

Figure 5. *Regions showing preference for FV > All. The regions identified include the bilateral fusiform gyri, the bilateral lingual gyri. and the posterior angular gyrus. Note- Image presentation is left-right inverted.*



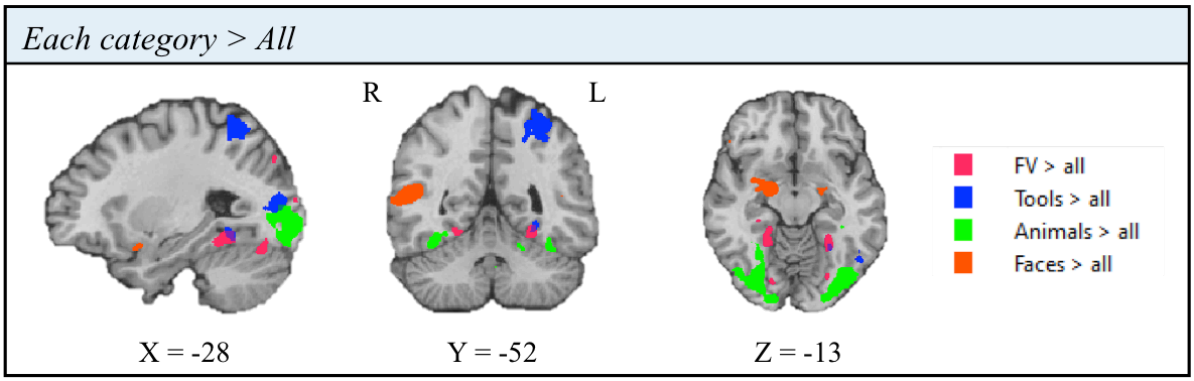
An exhaustive list of the activated regions and their corresponding peak voxels with significance values can be found in Table 5.

Table 5.
*Talairach coordinates for peak voxels from regions showing differential BOLD contrast for **FV > All***

Region	Hemisphere	Peak voxel coordinates (XYZ)			Statistical value for peak voxel	Volume (mm^3)
Superior Occipital Gyrus	Right	41	-76	28	$t_{(15)}$=5.75, p < .001	118
Middle Occipital Gyrus	Right	29	-94	6	$t_{(15)}$=5.27, p < .001	78
Parahippocampal Gyrus	Right	30	16	51	$t_{(15)}$=5.24, p < .001	126
Caudate	Right	29	-33	-14	$t_{(15)}$=6.48, p < .001	72
Fusiform Gyrus (medial)	Right	22	-51	-13	$t_{(15)}$=5.9, p < .001	360
Lingual Gyrus	Right	18	-81	-14	$t_{(15)}$=5.52, p < .001	195
Lentiform Nucleus	Right	17	3	-2	$t_{(15)}$=5.65, p < .001	42
Superior Frontal Gyrus	Right	17	39	34	$t_{(15)}$=4.99, p < .001	8
Posterior cingulate gyrus	Right	2	-43	36	$t_{(15)}$=4.77, p < .001	6
Posterior cingulate gyrus	Left	-1	-41	39	$t_{(15)}$=4.85, p < .001	15
Posterior cingulate gyrus	Left	-3	-39	24	$t_{(15)}$=5.52 p < .001	103
Fusiform Gyrus (medial)	Left	-27	-50	-14	$t_{(15)}$=6.45, p < .001	609
Lingual Gyrus	Left	-27	-73	-21	$t_{(15)}$=6.09, p < .001	414
Inferior Parietal Lobule (posterior angular gyrus)	Left	-35	-82	36	$t_{(15)}$=8.37, p < .001	350
Middle Occipital Gyrus	Left	-32	-94	12	$t_{(15)}$=4.98, p < .001	45
Parahippocampal Gyrus	Left	-30	-30	-18	$t_{(15)}$=5.16, p < .001	32

Each category > All. Contrast was performed for each category against all other categories to obtain a global picture of category-selective activation. This type of contrast was made to allow for a balanced comparison between FV and other categories in addition to adhering to the original method for localizing category-selective regions (Epstein & Kanwisher, 1998; Kanwisher et al., 1997). Figure 6 illustrates the contrast in activation of each category compared to the average of all other categories. There was overlap between the tool-preferring and FV-preferring regions of the left fusiform gyrus- specifically in the medial portion. Bilateral activation of the lateral fusiform gyrus was observed for the animal category, as has previously been shown (Chao et al., 1999). The right medial fusiform was also more active for FV, which was driven by the [FV > Tools] and [FV > Faces] contrasts.

Figure 6. *Regions showing preference for each category > All. Note- Image presentation is left-right inverted.*

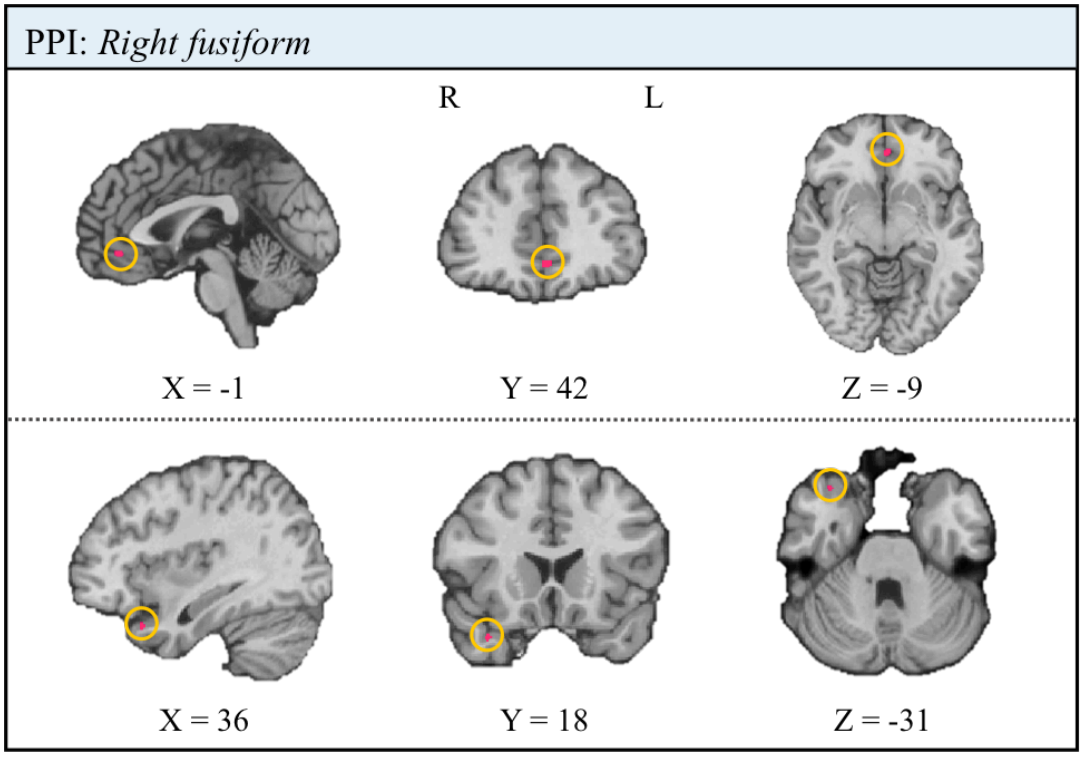


PPI. Whole-brain PPI analysis was conducted on five seed regions defined from the [FV > all] contrast. One-sample t-tests against chance (FDR < .05) indicated that three of the five seed regions resulted in significant clusters of positive connectivity in addition to several clusters of negative connectivity with the seed region. Negative findings suggest that as FV-selective activity was increasing in the seed ROI, activity was decreasing in these other areas. However, as negative PPI is difficult to interpret, an emphasis was placed on areas in which FV-specific positive connectivity was observed.

As can be seen in Figure 7, the right fusiform was positively connected with the ventromedial prefrontal cortex (vmPFC) and the right temporal pole. Both the vmPFC and temporal pole have been considered important areas in emotion processing (Binder & Desai, 2011). However, given the seed region's proximity to the fusiform face area, it was

important to rule out an effect being attributable to activation carry-over from this region. It was reasoned that if the Faces category was the driving factor, then a positive PPI should also emerge when Faces is considered. However, PPI analysis did not result in face-specific connectivity between these regions.

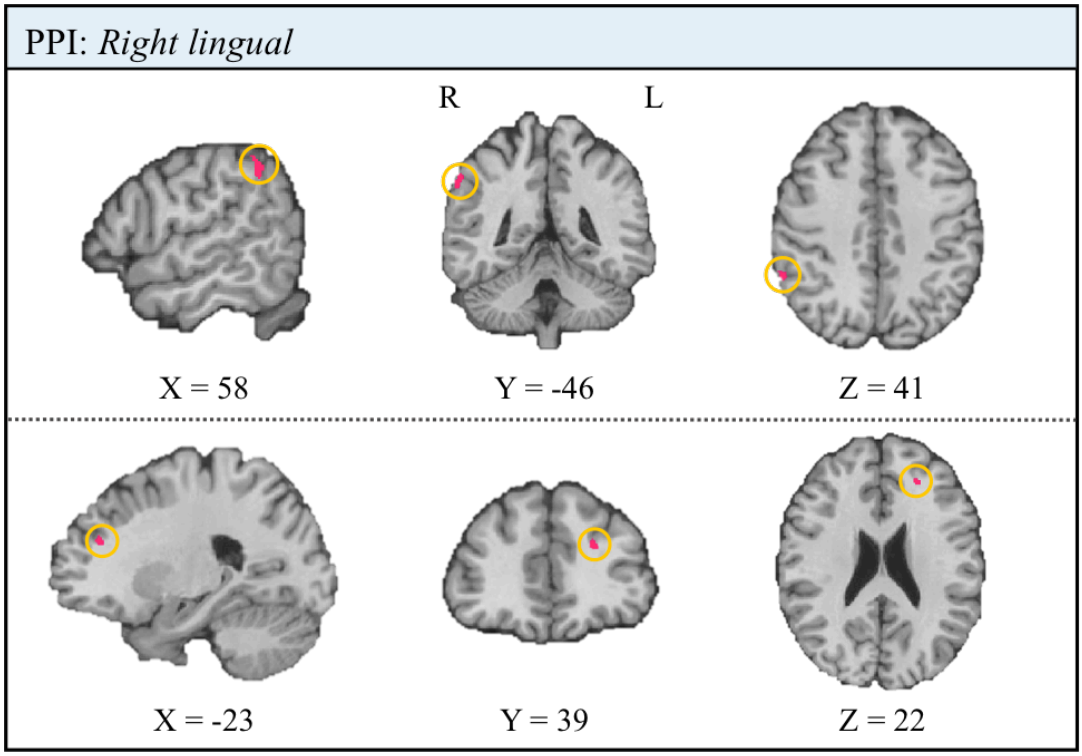
Figure 7. *PPI interaction with the right fusiform as seed region (identified from the contrast [FV > all]). Regions of significant connectivity (pink) are FDR-corrected at p < .05. Top panel- A significant cluster of positive connectivity with the seed region was found in the ventromedial prefrontal cortex. Bottom panel- A second cluster of positive connectivity with the seed region was found in the temporal pole.*



Positive connectivity was also found between the right lingual gyrus and the right supramarginal gyrus (see Figure 8). Interestingly, the supramarginal gyrus has been not

only associated with the processing of nonliving entities (Martin et al., 1996), but the right supramarginal, in particular, has been linked to spatial processing (Stephan et al., 2003). In addition, there was positive connectivity again with the left dorsal medial prefrontal cortex (dmPFC), an area that has consistently been activated in semantic studies although largely overlooked, with deficits to this region affecting goal-directed retrieval of semantic information (Binder, Desai, Graves, & Conant, 2009).

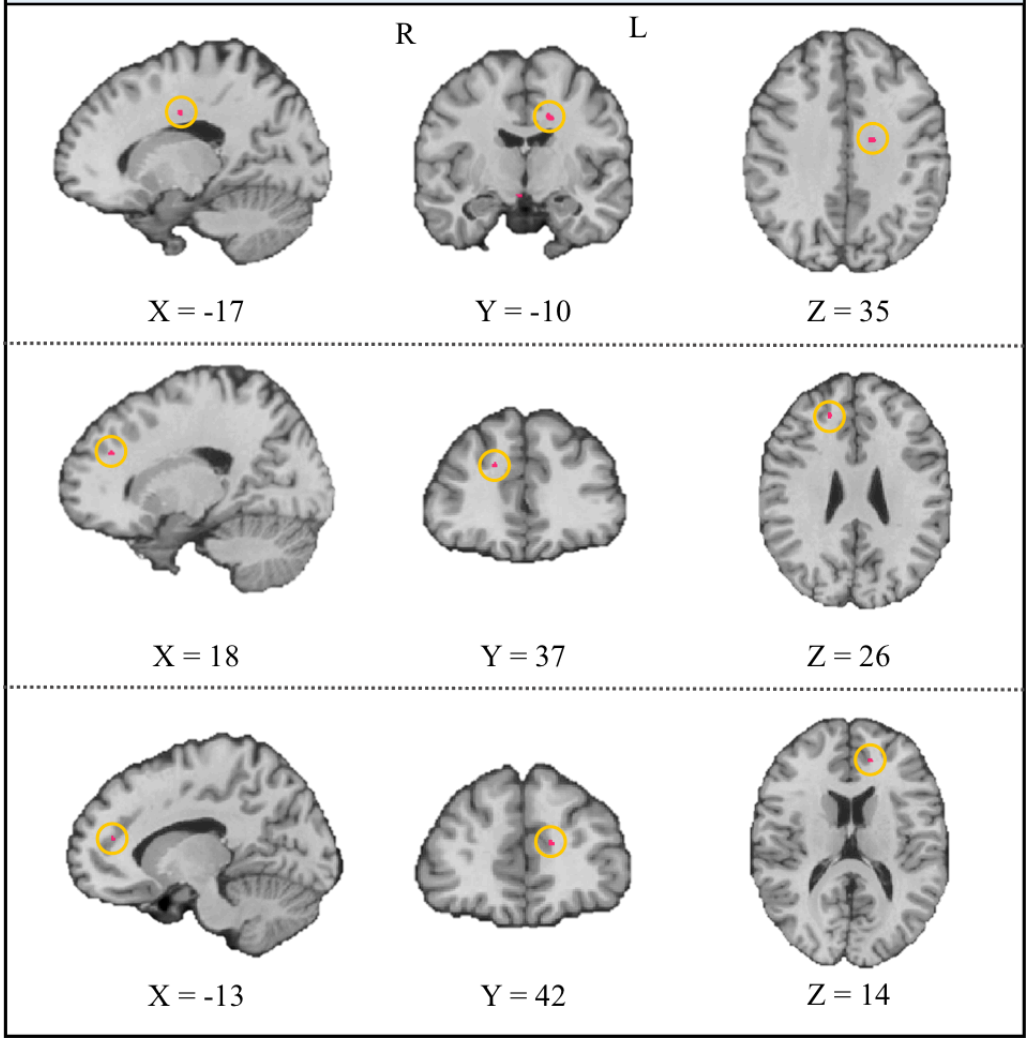
Figure 8. *PPI interaction with the right lingual gyrus as seed region (identified from the contrast [FV > all]). Regions of significant connectivity (pink) are FDR-corrected at p < .05.* *Top panel*- *A significant cluster of positive connectivity with the seed region was found in the right supramarginal gyrus.* *Bottom panel*- *A second cluster of positive connectivity with the seed region was found in the left dorsal medial prefrontal cortex.*



Finally, the left lingual gyrus showed positive connectivity with the posterior cingulate cortex (see Figure 9). The posterior cingulate cortex has been implicated in perceptually-encoded knowledge such as concreteness of an object (i.e., based in sensorimotor experience; Fliessbach, Weis, Klaver, Elger, & Weber, 2006; for a review, see Binder, Desai, Graves, & Conant, 2009). Additionally, a significant cluster of activation was found in the right dmPFC as well as in the left vmPFC. Generally, a few of the clusters of connectivity were found within white matter regions, specifically when the lingual gyrus was used as a seed region. When checked in the Talairach atlas, all but one significant cluster (that connecting the lingual gyrus with the cingulate cortex) was found within $3mm^3$ of the gray matter region identified. While it is important to cautiously interpret such a finding, connectivity within white matter regions could also be the result of measurement error, potentially due to smoothing (6mm kernel) or less likely, to imprecise motion correction.

Figure 9. *PPI interaction with a portion of the left lingual gyrus as seed region (identified from the contrast [FV > all]). Regions of significant connectivity (pink) are FDR-corrected at p < .05. Top panel- A significant cluster of positive connectivity with the seed region was found in the left posterior cingulate cortex. Middle panel- A significant cluster of positive connectivity in the right dorsomedial prefrontal cortex. Bottom panel- A significant cluster of positive connectivity in the left ventromedial prefrontal cortex.*

PPI: *Left lingual*

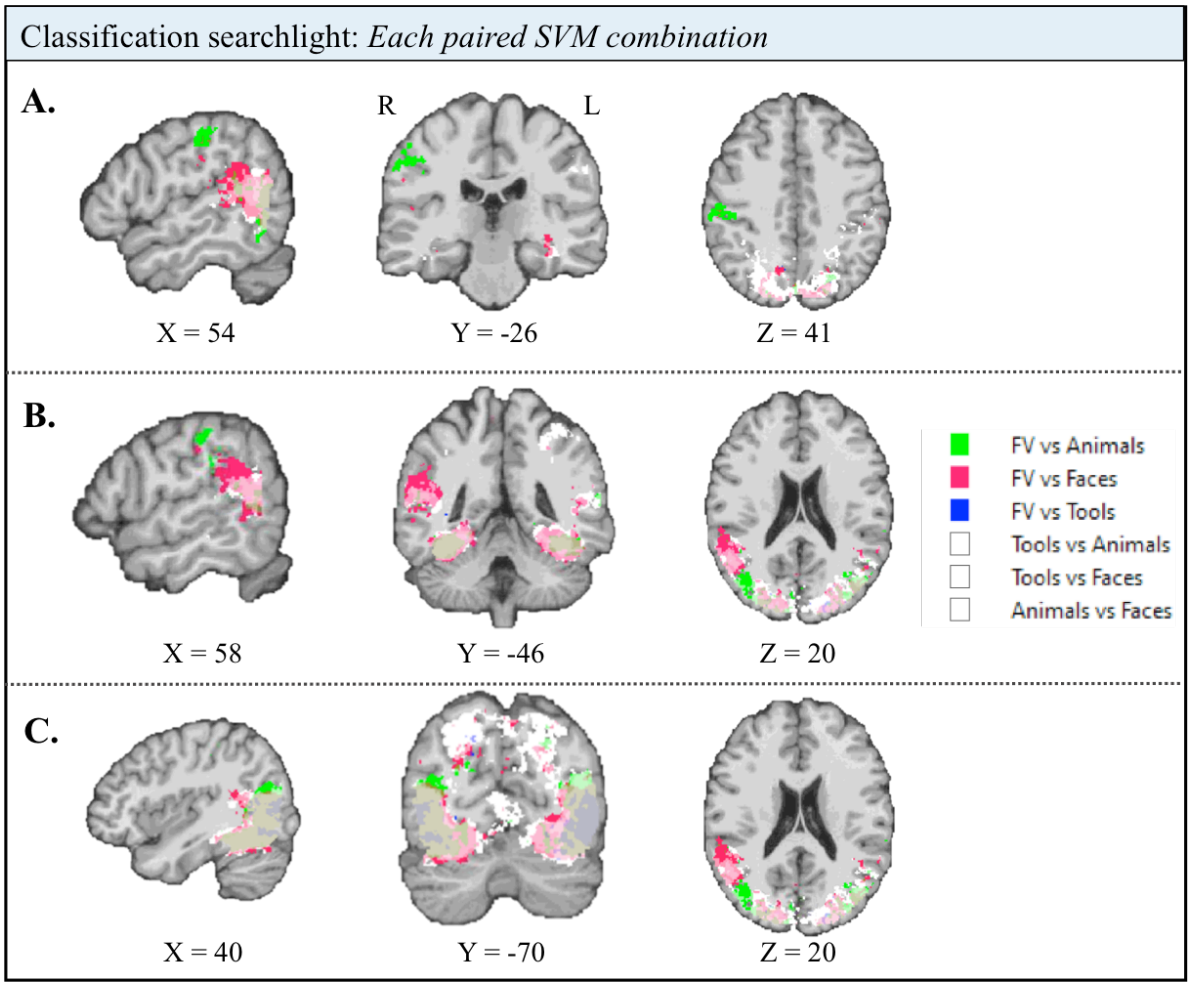


MVPA Classification searchlight. To map the discriminability between FV and each of the categories in the brain, a searchlight approach was used that recorded the accuracy of the SVM pattern classifier for each categorical pairing with the FV category, resulting in three classification maps (FV vs. Tools, FV vs. Animals, FV vs. Faces). Additionally, the three other categorical pairings (Tools vs. Animals, Tools vs. Faces, and Animals vs. Faces) were also subjected to SVM classification in order to resolve difficulty in being able to deduce preferential categorical processing from the FV-containing combinations alone.

This resulted in six classification maps that were superimposed and analyzed for regions of overlap in which 1.) the classifier correctly distinguished between FV and each of the other categories *and* 2.) the classifier could not distinguish between other categories belonging to combinations not containing FV, in order to ensure that a region was not carrying information for another category. As no region emerged that satisfied both of these two criteria, we considered areas of significant accuracy for each FV-containing map separately, so long as those regions didn't successfully discriminate between categories of non FV-containing pairings.

Three main regions emerged from classification analysis as are illustrated in Figure 10. A region of the right postcentral gyrus, slightly superior to the rostral portion of the supramarginal gyrus successfully discriminated between FV and Animals. Located in the primary somatosensory cortex, this region is prominent in the processing of touch as well as its integration with appropriate motor output (Borich, Brodie, Gray, Ionta, & Boyd, 2015). A second region was identified in the right supramarginal gyrus, particularly for the discrimination between FV and Faces. A third region successful in discriminating between FV and Animals was found in the right posterior middle temporal gyrus (pMTG). The pMTG has been broadly implicated in tasks of semantic control and tracking knowledge related to conceptual associations (for an overview, see Davey et al., 2016); additionally, it's involved in tool processing (Chao et al., 1999) and nonbiological motion (Stevens et al., 2015).

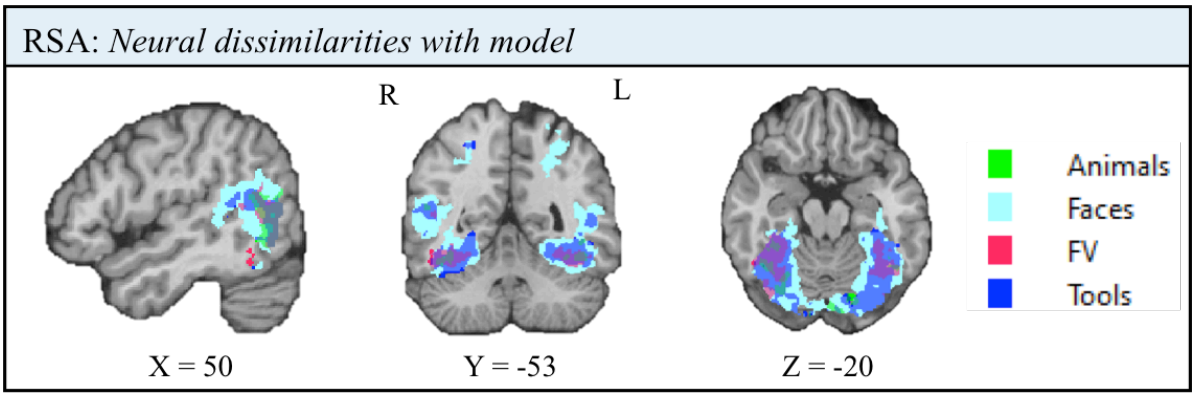
Figure 10. *Searchlight SVM classification accuracy maps for each of the 6 categorical pairings, thresholded at p < .01. Top panel- A significant cluster of voxels was found in a region of the right postcentral gyrus, mainly for the discrimination of [FV vs. Animals]. Middle panel- A significant cluster of voxels was found in the right supramarginal gyrus, mainly for the discrimination of [FV vs. Faces]. Bottom panel- A significant cluster of voxels was found in the right posterior middle temporal cortex, for the discrimination [FV vs. Animals].*



RSA Searchlight. Categorical models were created and correlated with neural dissimilarities across the brain in order to identify voxels that demonstrated significant categorical preference. The resulting z-maps were superimposed and inspected for significant regions with activity patterns uniquely representing FV. A cluster in the right

lateral fusiform gyrus was identified for which the neural dissimilarities significantly correlated with the FV model (see Figure 11).

Figure 11. *RSA searchlight classification accuracy maps for each of the 4 categories, thresholded at p < .05. A cluster of voxels for significant correlation between the FV model and neural dissimilarities was found in the lateral fusiform gyrus.*

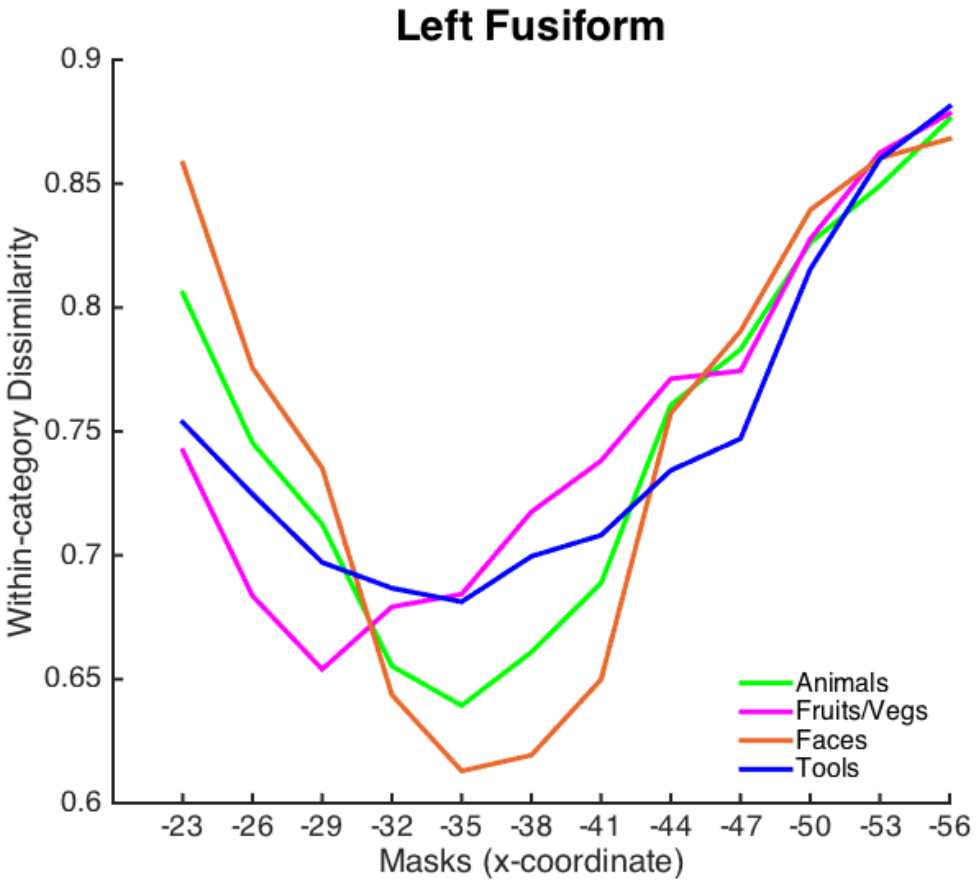


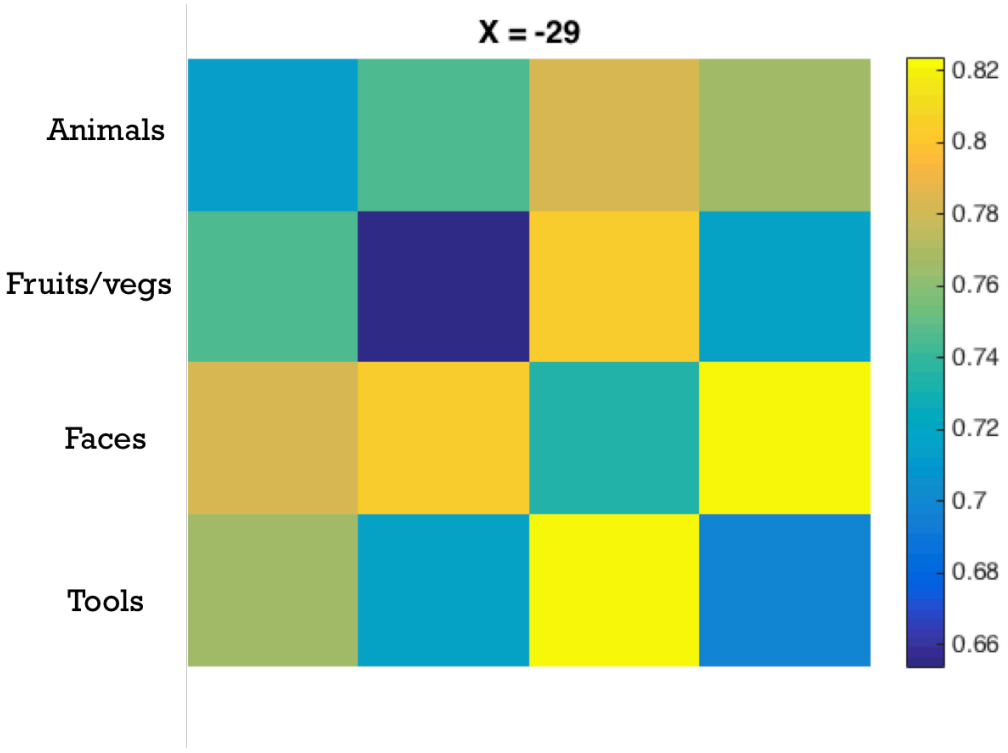
Given the prominent role that the fusiform has played in the semantic literature, its consistent activation/involvement in the current experiment, and the living yet 'inanimate' nature of fruits/vegetables, neural dissimilarities were explored based on a medial-to-lateral gradient as has been previously identified (Connolly et al., 2012; Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Chao et al., 1999). The purpose of exploring this gradient was to see if fruits/vegetables may be processed closer to the tool (inanimate) or animal (animate) region of the fusiform. An approach similar to that of Mahon and colleagues (2009) was adopted for segmenting the fusiform along the x-dimension and performing RSA on each slice separately. The area of the fusiform corresponding to categorical activation was first isolated by the contrast all categories > fixation. Next, a bounding box was created based on peak activations in the literature (for

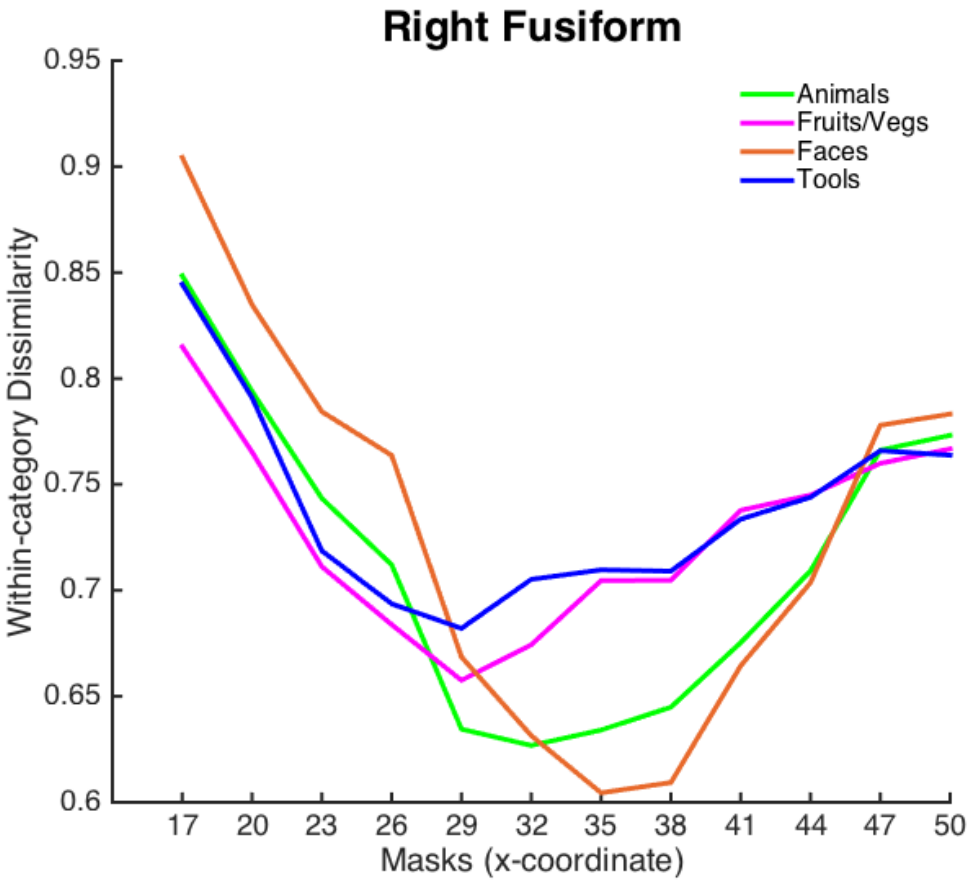
the y-dimension) and anatomical constraints (for the z-dimension). Slices of 3-mm in width were then created along the x-axis and neural dissimilarities calculated. Dissimilarities were determined per participant based on the correlations between the beta values for each miniblock. The mean within-category correlations were then averaged across all participants (see Figure 12). Interestingly, the most medial portions of the left and right fusiform displayed the lowest dissimilarity for FV relative to the within-category and between-category dissimilarities of each of the other categories. In particular, FV demonstrated a trough of dissimilarity between x = -29 and x = -32, corresponding to the medial portion of the left fusiform. Animals and faces exhibited a similar trough between x = -35 and x = -41, corresponding to a lateral portion. Although a medial bias for FV was more pronounced in the left fusiform, the right fusiform also displayed this preference relative to the other categories. More generally, the patterns of dissimilarity across both the left and right fusiform are most similar for FV and tools and then for animals and faces. Furthermore, if we consider the between-class dissimilarity, FV are more similar to tools than they are to the other categories in this region (see lower panel of Figure 12). It appears from the neural dissimilarities that the medial fusiform demonstrates higher within-category dissimilarity for FV although the model-based RSA approach would suggest that the lateral right fusiform more highly correlates with an FV-selective model. Although prima facie incompatible, it should be considered that the model-based approach implemented searchlight, which involved a different subset of voxels for calculation. Segmentation of the fusiform was defined as a specific region with a larger expanse then the y- and z-coordinates identified by the model. It could be that, by comparison to the other categories, FV was still preferred in a more lateral right fusiform region, although

not possessing low dissimilarity; as can be seen from Figure 12, dissimilarities for all categories increased around x = ± 50, which aligned with the x-coordinate for the patch of lateral right fusiform that was FV-model selective.

Figure 12. *RSA for each of the 4 categories across the x-dimension of the fusiform. Lower values constitute lower dissimarlity within the category. Upper panel: Dissimilarities for each category are plotted for each slice (mask) of the left fusiform. Middle panel: The confusion matrix of dissimilarities both within and between categories. Note that the within-category dissimilarity for FV is lower than the any of the other within-category or between-category dissimilarities. Lower panel: Dissimilarities for the right fusiform. Note: There is a shift in the categorical activation between the left and right fusiform, with the right fusiform shifted 6 coordinate points more medial than the left fusiform.*




X = -29
Animals
Fruits/vegs
Faces
Tools
0.82
0.8
0.78
0.76
0.74
0.72
0.7
0.68
0.66


Right Fusiform
Animals
Fruits/Vegs
Faces
Tools
Within-category Dissimilarity
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
17
20
23
26
29
32
35
38
41
44
47
50
Masks (x-coordinate)

Discussion

The current experiment utilized a functional localizer task to investigate the neural correlates associated with the processing of FV. To this end, contrast analysis was combined with connectivity measures as well as neural pattern analysis to elucidate a potential network of regions responsible for the conceptual processing of FV. Contrast analysis revealed a number of regions that were more active for FV than the average across other categories, these regions comprising the bilateral lingual gyrus, the bilateral fusiform gyrus and the left angular gyrus.

The lingual gyrus contains the posterior area of V4, which is shown to be integral to color processing due to the strength of response of its receptive fields (Bartels & Zeki, 2000), attentional filtering of color information (Roe et al., 2012), and acquired color blindness linked to lesions in this region (Shuren, Brott, Shefft, & Houston, 1996). Its involvement in the current study is particularly interesting given the fact that all images were presented in grayscale; therefore, despite color being an important property for the categorization of FV (as exemplified in Chapters 1 and 2), activation of this region cannot be due to physical object color. Although it was difficult to match categories for features such as spatial frequency and size, due to intrinsic differences in object representations, the category of FV fell within the middle range of values and consequently, rendering it unlikely to elicit differential activation based on low-level visual properties. Due to its connectivity with higher-level object processing regions in the ventral temporal cortex, such as the fusiform gyrus and the parahippocampal gyrus (Aminoff et al., 2014), a highly

plausible explanation is that it is involved in the conceptual processing of FV given the importance of color to its identity. The claim is not that the lingual gyrus is necessary or sufficient for the processing of FV, but could be the result of an integration between top-down and bottom-up influences; it has been proposed that higher-level regions in the fusiform representing knowledge for color can reactivate lower-level sensory processing regions (Aminoff et al., 2014). As V4 has been linked to feature-based attention and is sensitive to contextual modulation (Roe et al., 2012), activation could be due to salience of processing of the FV category linked with properties critical to its representation. One important biasing mechanism can be internally-generated goal-directed attention; given the evolutionary importance of FV to survival, it could be that attentional salience is automatically generated, thereby linking the stimulus with properties that sustain goal-directed action (Desimone & Duncan, 1995).

Apart from the role of the posterior V4 in color processing, a more anterior portion of the V4 that extends from the medial fusiform gyrus has been considered a second color center (Bartels & Zeki, 2000). This region has demonstrated more selective color processing-specifically, activity is observed for colored objects but not for colored abstract scenes (Zeki & Marini, 1998). Studies of semantic processing have distinguished between regions involved in color perception versus those involved in object-associated color knowledge, informed by case studies that have demonstrated dissociations between the two; patients with lesions to the lingual gyrus have been impaired in color perception yet can generate color imagery (Shuren et al., 1996) whereas those with lesions to the ventral temporal cortex (relatively more anterior) have been impaired in object color knowledge (Miceli et

al., 2001). Additionally, activity in the fusiform gyrus has been linked to the retrieval of object-associated color knowledge in healthy participants (Simmons et al., 2007). It would appear that the nuanced processing of color along the ventral-occipital-temporal cortex progresses from low-level perceptual processing in posterior regions to an integration with higher-level object processing and conceptual knowledge in more anterior regions; this processing extends downstream into regions like the fusiform gyrus, which is well-established in the literature regarding its role in category-specific processing (for reviews, see Kanwisher, 2010; Martin, 2007).

Selective activation for FV was also observed in the bilateral fusiform, interestingly, in the medial portion. Apart from contrast analysis, RSA revealed that the neural patterns representing FV demonstrated the lowest dissimilarity in the medial portion of the left fusiform, even greater than that of tools. Critically, patterns of similarity across both the left and right fusiform represented a coupling between FV and tools and between animals and faces, with fruits/vegetables being more dissimilar to tools than to animals or faces. The left medial fusiform gyrus has typically been considered a region involved in the processing of tools (Chao et al., 1999) displaying functional connectivity with more inferior regions of the left parietal cortex, and part of the more extensive left-lateralized tool processing network (Garcea & Mahon, 2014). This network has been parcellated into several parts depending on the type of knowledge represented (e.g., visually-guided reaching, grasping, goal-directed action, surface-texture information). The fact that tools are considered manipulable entities is a critical aspect to such a distributed knowledge network. Similarly, fruits/vegetables share this property, with some studies analyzing

motor affordances for the processing of graspable objects irrespective of their membership to the natural or artificial domain (Netelenbos & Gonzalez, 2015). However, a vast majority of the literature seems to have linked the property of manipulability to man-made entities. From the perspective of motion processing, biological/human motion (Bonda et al., 1996) has been distinguished from motion related to artifacts (Beauchamp et al., 2002). However, if we consider biological motion as the ability to exert endongenous movement without facilitation from an external agent, then a mere distinction along the natural/artificial axis does not suffice. Fruits/vegetables are more similar to tools in this regard, such that they require exogenous manipulation to be *acted-on*. Within this framework, it is unsurprising that FV should activate regions that are implicated in tool processing, given this critical aspect to their representation. Indeed, in the current study, the results across analyses converged to support overlap between canonically tool-preferring and FV-processing regions. Apart from the lingual and fusiform gyri, contrast analysis revealed activation in the angular gyrus, which has been associated with the grasping phase of tool use (Creem-regehr & Lee, 2005). Furthermore, SVM searchlight classification demonstrated that a successful distinction between FV and animals could be found in the postcentral gyrus and the right posterior middle temporal gyrus and a distinction between FV and faces in the supramarginal gyrus. These regions, although right-lateralized, have also been considered as integral components to motor and tool processing. The postcentral gyrus, located in the primary somatosensory cortex, is responsible for the processing of touch as well as its integration with appropriate motor output (Borich et al., 2015). The supramarginal gyrus has been associated with the processing of nonliving entities (Martin et al., 1996) and retrieval of object-associated

manipulation knowledge (Mahon et al., 2007; Rumiati et al., 2004); the right supramarginal, in particular though, has been linked to spatial processing (Stephan et al., 2003). The posterior middle temporal gyrus has been broadly implicated in tasks of semantic control and tracking knowledge related to conceptual associations (for an overview, see Davey et al., 2016) in addition to its involvement in motion-processing particularly related to tools (Martin & Chao, 2001). Given that fruits/vegetables are considered to be natural entities along with faces and animals, it is highly plausible that these regions are fundamental in processing aspects of fruits/vegetables that are not shared by the other categories- namely, the automatic engagement of motor representations in their conceptual processing.

Beyond the role of the angular and supramarginal gyri in aspects of tool processing, some have suggested their involvement in a bottom-up subsystem of attentional allocation towards task-relevant stimuli (Ciaramelli, Grady, & Moscovitch, 2008); the angular gyrus, particularly, is considered to be involved in the reorienting of spatial attention due to stimulus salience, incorporating information related to the motor response, emotional valence, and category membership of a given stimulus (Gottlieb, 2007). Due to the importance of food for survival, it is likely that the category of fruits/vegetables possesses a strong attention-capturing effect, integrating information from various modalities to subserve the automatically generated end goal of ingestion. Supporting this framework, PPI analysis demonstrated significant FV-dependent connectivity within a number of regions involved in higher-order cognition linked with attention, emotion, and reward-processing. PPI analysis revealed significant FV-specific connectivity between the right

lingual gyrus and the right supramarginal gyrus, in addition to the dmPFC. The dmPFC has also been consistently activated in the semantic literature, and postulated to be involved in self-guided, goal directed semantic retrieval with recruitment in networks of sustained attention (Binder et al., 2009). The left lingual gyrus also demonstrated FV-specific connectivity with the bilateral prefrontal cortex in addition to the posterior cingulate cortex. The posterior cingulate cortex belongs to the main regions responsible for semantic retrieval, including a likely role in integrative processes, serving as an interface between unimodal and heteromodal processing areas (Binder et al., 2009). Given the importance of visual feature processing of the lingual gyrus, potential attentional components of the supramarginal gyrus and dmPFC, it is likely that the processing of FV engages a network of regions employed for visually guided goal-directed action.

PPI analysis also revealed significant connectivity between the right fusiform gyrus and the vmPFC and temporal pole, particularly for the FV category. The vmPFC has been associated with motivation, decision-making and reward processing (Binder et al., 2009), with some research showing a particular involvement in food perception (Rolls, 2015). The temporal pole has also been linked to processing of stimuli with strong emotional valence, bearing strong projections to the prefrontal cortex (Olson, Plotzker, & Ezzyat, 2007). A meta-analysis by Van Der Laan and colleagues (2011) found that the bilateral posterior fusiform and left orbitofrontal cortex were among the most prominent regions activated in the viewing of food images. Stronger activations were also witnessed in the lateral occipital complex; beyond its general role in object recognition (Grill-Spector & Weiner, 2014), it was posited that emotionally-salient stimuli like food lead to an increase

in attention and enhancement of visual processing (Killgore & Yurgelun-Todd, 2007). The role of emotion in salience processing for the FV category could also explain why the results of the current experiment favor a right-lateralized network, given a right hemisphere hypothesis in the general domain of emotional processing (Borod et al., 1998). Although contrast analysis showed bilateral activations in the fusiform and lingual gyri, in addition to the left angular gyrus, classification and neural pattern analysis revealed processing in the right posterior middle temporal gyrus, supramarginal gyrus, and postcentral gyrus, regions analogous to the left-lateralized tool-processing network that are yet involved in aspects of spatial and motor processing. Interestingly, although the medial portions of the fusiform gyrus demonstrated highest within-category correlation for the neural patterns representing fruits and vegetables (predominantly in the left fusiform), model-based RSA analysis revealed a portion of the right lateral fusiform that displayed significant correlation between the FV-preferring model and neural dissimilarities. Furthermore, this region is proximal to the fusiform face area (FFA). One theory could be that in order to resolve between-category similarity for correct categorical identification, recruitment of resources will be a function of the magnitude of this similarity. As faces usually elicit activity in regions that are also involved in attention and emotional processing, similar to those observed for FV (e.g., prefrontal cortices, cingulate gyrus), preferential activity for FV at a region close to FFA could be the reflection of exertion of top-down regulatory processes for categorical distinction.

A synthesis of the current findings suggests three important aspects to the automatic processing of fruits/vegetables- 1.) the activation of visual feature processing regions,

particularly those responsible for color, 2.) the activation of regions typically associated with spatial and motor processing, particularly for grasping, and 3.) the activation of attention/emotional processing regions that may be endogenously triggered due to the importance of FV to survival and may consequentially exert a top-down influence on unimodal processing regions. The integration of both visual and motor properties via an attention biasing mechanism can lead to the distributed network of regions seen here. The fact that patient profiles have demonstrated diverging patterns of deficit for fruits/vegetables, rendering difficulty in mapping them onto the living/nonliving dichotomy, could be due to features from both categories being integral to their processing. Depending on the lesion site and its interference in network processing, the FV category could display impairment along with other natural entities or with man-made artifacts.

While the present experiment offers insight into the automatic activation of a fruits/vegetables processing network, it is limited in that regional activation only concerns processes engaged in passive viewing. It is difficult to discern how motor-processing regions such as more superior portions of the parietal lobule and motor cortices would respond to actual reach-to-grasp behavior related to fruits/vegetables versus tools. Furthermore, given the size of the fusiform and the purported nature of categorical processing along a medial-to-lateral gradient, in order to better establish connectivity with other regions, it may behoove to use partial correlation in order to eliminate any influence from other cortical regions (Zhang et al., 2008). However, the current study has offered a step in identifying a formalized network for the processing of fruits/vegetables that

supports the engagement of feature-based processing regions and modulatory influences by attention/emotional biasing mechanisms that exert top-down control.

GENERAL DISCUSSION

Semantic memory encompasses the entirety of general world knowledge- the conceptualization of everything that can be abstracted from experience without reference to any one specific experience (Binder & Desai, 2011). Given the extensiveness of what it entails, theories as to the organization of its contents and its direct mapping to specific neural correlates in the brain have proven to be equally as vast. Early neuropsychological case studies demonstrated diverse patterns of deficits across different categorical domains that posed challenging questions as to the division of the semantic system that are still relevant today. Of these, whether or not the structure of semantics emerges from categories adhering to certain boundaries as an organizing principle or from categorical representations relying on different attribute types remains a central concern.

One core focus of the current body of work was to explore the interaction between two specific subcategories within the broad living/nonliving dichotomy of semantics- namely fruits/vegetables and tools, and the properties differentially relevant to their processing- color and orientation, respectively. Particular emphasis was given to the category of fruits/vegetables, which has demonstrated a pattern of deficit rendering it unreliably mapped onto either the living or nonliving domain (Blundo et al., 2006; A. Caramazza & Shelton, 1998; Hart et al., 1985; Hillis & Caramazza, 1991). By all accounts of conceptual organization, fruits/vegetables, are particularly intriguing due to their importance to survival (Mahon & Caramazza, 2011), purported high color diagnosticity (Humphreys & Forde, 2001), and similarity of within-category membership (Tyler et al., 2003), theoretically rendering them privileged in evolutionary status and sensitive to feature type.

In light of these elements, chapters one and two focused on the features relevant to the automatic categorization of fruits/vegetables versus tools, both at the behavioral and neural level, and chapter three on elucidating a network for the processing of fruits/vegetables.

Findings from chapter one indicated that fruits/vegetables and tools rely on different features for their processing- namely, color for the former and orientation for the latter- as indexed by a lexical identity priming paradigm; moreover, these features are automatically associated with the conceptual representations of each even in the absence of overt instructions to compare prime-target relatedness. Furthermore, the observed graded priming effect of feature modification with respect to the category, largely supports a sensory/functional theory of semantics, due to a sensitivity to modality. Interestingly, the effect of feature modificiation could not have directly interfered with low-level visual processing given the cross-modal approach adopted, with responses made to the word target. Taken together, our findings demonstrate an automatic activation of modality-specific processing in the conceptual representation of fruits/vegetables and tools. This automaticity at the behavioral level was corroborated by the results of chapter 2 in which the neural response within the N400 time window significantly differed between normal and feature-modified conditions that were most critical to the category (i.e., color for fruits/vegetables and orientation for tools). The results suggested a semantic violation that was induced by the prime manipulation of a category-relevant feature. This finding again provides compelling evidence for color and orientation being processed as conceptual "primitives", or properties fundamental for the rapid identification of objects at the basic level of categorization (Martin, 2016).

Chapter three explored a network for the processing of fruits/vegetables through a passive viewing localizer task, with activations observed in regions associated with category-processing (i.e., fusiform gyrus) as well as more fine-grained processing of color and motion along the ventral temporal and parietal cortices. In addition, connectivity and neural pattern analysis revealed regions associated with attention and reward-processing that were selectivity involved in the processing of fruits/vegetables. One plausible explanation for these findings is that, due to their importance to survival, fruits/vegetables are highly salient and automatically engage attentional mechanisms that lead to top-down modulation of modality-specific regions critical to their recognition.

One surprising finding was the greater within-category correlation for fruits/vegetables in medial portions of the fusiform, which has reliably been associated with tool processing. This provides strong indication that, apart from right-lateralized supramarginal and angular gyri activation that could be the result of attentional reorienting (Ciaramelli et al., 2008), fruits/vegetables may activate motor representations that facilitate implicit grasp-to-reach goal-directed behavior. A synthesis of findings with the other two chapters would suggest that fruits/vegetables, although more dependent on color for their semantic representation, may also activate motor-relevant regions as, although formally biological, they necessitate being acted upon to fulfill their "survival-sustaining" role (e.g., render them edible to be eaten). Although within the category of fruits/vegetables, it could be argued that some items engage motor processing more than others (e.g., a banana may necessitate more manipulation than a grape), it could be that fruits/vegetables are more strongly associated

with the category of "food" than other categories might be to their superordinate category membership. Thus, when individual exemplars are considered, such as in the case of the EEG experiment, there may be more variability from trial-to-trial, whereas in the fMRI localizer task, the rapid visual presentation in a block design could have more generally activated a 'food' representation.

The category of fruits/vegetables, with its multidimensional representation, is of the most fascinating in semantics. Not only multi-sensorial in nature, it possesses properties that traverse perceptual-, motoric-, and emotional-processing domains. It is perhaps due to this richness of representation, which may translate to a complexity of processing, that has made it particularly difficult to elucidate its contents and pinpoint its place in semantics. With advancements in neurophysiological techniques that have provided insight into the structure of semantics at an unparalleled resolution, the picture will surely become clearer. The current work has endeavored to make a small contribution towards this end.

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